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BIOGEOGRAPHY OF UPLAND BIRD COMMUNITIES IN THE PERUVIAN AMAZON

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BIOGEOGRAPHY OF UPLAND BIRD COMMUNITIES IN THE PERUVIAN AMAZON

by

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DEDICATION

To my family

and

To the young Peruvian ornithologists

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BIOGEOGRAPHY OF UPLAND BIRD COMMUNITIES IN THE PERUVIAN AMAZON

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The western Amazon is known to be one of the most biologically diverse regions in the world, yet information about the spatial distribution of that biodiversity and the processes governing its distribution remains scarce. An improved understanding of those biogeographic patterns and processes can inform conservation and development planning in areas where anthropogenic landscape change is ongoing. Spatial components of biodiversity are known to be influenced by historical and present-day physical and human geographic processes. There is evidence that major Amazonian rivers form the boundaries of biological regions, at least for birds. Other factors that may influence bird species composition include the dispersal limitations of individual species, forest plant species composition and structure, topography, forest fragmentation, and hunting.

Sites where bird species composition was measured in this study represented mature, upland forest on both sides of the Amazon River, and a range of non-flooded forest types, as indicated by soil and plant surveys. Bird species compositional variation was closely correlated with variation in plant species composition, human disturbance associated with forest fragmentation, and position north or south of the Amazon River. The strongest differences were between opposite sides of the river, even though local environments, including plant composition, were not different on the two sides. This strongly suggests that historical biogeographic factors, rather than present-day environmental gradients, are responsible for bioregional boundaries at Amazonian rivers. The difference between plant and bird distributions at this scale underscores the pressing need to re-evaluate general notions of bioregional complexity and pattern in the Amazon basin.

Locally, the influence of habitat fragmentation on animal communities, including reduced species richness, was confirmed. The influence of local floristic variation is of particular importance due to its ubiquity across western Amazonia. Thus, understanding the distributions of soils and vegetation is critical for explaining Amazonian animal diversity. The use of these factors to model bird community heterogeneity contradicts assumptions that the processes shaping Amazonian animal community diversity are too complex to measure efficiently, and their use contributes a new understanding of the dimensions of that diversity.

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Chapter One

Avian Biogeography of the Western Amazon Basin

The most fundamental biogeographic questions concern how biological populations and communities are distributed across landscapes and regions, and what processes influence their distributions. For some of the most biogeographically interesting places on Earth, these basic questions remain largely unanswered. The western Amazon basin is certainly among those places—it harbors the highest local species diversities on the planet, but the geographical characteristics of that diversity have only recently begun to be described in much detail (Tuomisto 1998, Lomolino and Heany 2004, Schulman et al. 2007). Nonetheless, progress is being made. Recent advances in the biogeography of Amazonian plants suggest that the number of unique forest types in the western Amazon is very high, indicating complex heterogeneity at a variety of spatial scales (Tuomisto et al. 1995, Phillips et al. 2003, Tuomisto et al. 2003a, Phillips et al. 2004, Valencia et al. 2004, ter Steege et al. 2006, Pitman et al. 2008). The consequences of this heterogeneity for Amazonian animal species remain to be fully explored.

Here I discuss what has been learned about the spatial heterogeneity of Amazonian bird communities, emphasizing the importance of multiple natural and anthropogenic processes at multiple spatial extents from the continental to the very local.

Specifically, I review progress in the avian biogeography of the western Amazon basin, drawing from several related fields to suggest an agenda for integrated future research. I have made no attempt to exhaustively review the literature in each area covered. Rather, I use relevant published work to represent research agendas, problems, controversies, and progress, and to point in the particular research direction that this dissertation takes. The specific questions addressed by my dissertation research are detailed in Chapter Three.

The biological diversity of complex present-day landscapes has resulted from, and constitutes, a large number of overlapping and interacting factors, and successful interpretations of those relationships will need to draw on geology, geomorphology, climatology, biogeography, and ecology at a minimum, and must investigate the past as well as the present (Schluter and Ricklefs 1993, Tuomisto and Ruokolainen 1997, Cowell and Parker 2004, Young et al. 2004, Ricklefs 2006, Young and Aspinall 2006). Potentially important factors can be identified along multiple spectra: historical to present-day, evolutionary to ecological, anthropogenic to natural, and local to continental. While the full analytical integration of large numbers of important factors is far from tractable, an explicitly integrative approach is nonetheless useful because the influences of disparate factors can be measured comparatively, and their interactions assessed.

This review is organized in terms of the factors that researchers have considered important for the spatial diversification of bird communities. Those factors can be loosely categorized as evolutionary and ecological, with anthropogenic effects as an important category of ecological factors, and I consider them in that order. Spatial scale considerations are noted throughout, and are further addressed in the concluding section.

It should of course be noted, despite my categorization scheme, that ecology and evolution are not functionally separate phenomena in nature. Evolutionary diversifications have been caused in large part by historical ecological conditions (Grant and Grant 2008, Price 2008, Schluter 2009). Modern ecological conditions, including human activities, are in turn shaped by the biological diversity that evolution has generated. Recognizing the holism of biogeographic phenomena, though, should not detract from the usefulness of identifying specific relationships among specific phenomena. Indeed, I attempt here to highlight the utility of taking a larger view that is informed by a large number of more narrowly focused analyses.

PHYSICAL GEOGRAPHY AND AVIAN EVOLUTION AND TAXONOMY

The geology, geomorphology, hydrology, and climate of northern South America have shaped Amazonian biogeography in two crucial ways. First, the changing character and distribution of landforms and water bodies, and therefore of biological habitats, over geologic time scales has played a critical role in the evolution of Amazonian taxa, producing the regional species pools that exist today. Second, those same processes are responsible for the current distribution of Amazonian habitats, which profoundly affects which of those species occur where, in the ecological short term. These short-term distributional patterns may also, of course, be active agents in the continuing evolution of species.

Continental biogeographic zones evident in Amazonian bird species distributions, along with numerous speciation events themselves, have been attributed by a number of researchers to the influence of historical climatic variability on the distributions of habitats (e.g., Fjeldsa 1994, Haffer 1997, Colinvaux 1998, Hooghiemstra and Van der Hammen 1998). Attention has been focused primarily on climatic changes during the Pleistocene, but the approach is relevant for all geologic time periods when evolutionary events of interest may have occurred, and for geomorphologic change as well as climatic change. More recent research has stimulated special interest in Miocene and Pliocene events, which may have been of particular importance for species-level diversifications in northern South America. The first part of this review is focused on the historical processes that have shaped western Amazonian avian diversity, but a word about taxonomy is in order first.

Amazonian bird systematics and the timing of evolution

Any biogeographic assessment is predicated on taxonomic description. Before the distributional limits of a taxon, or the diversity of a community, can be described, taxonomic units such as genera, species, and subspecies must be defined. Because avian systematics is a dynamic field with revisions and additions being made continually, biogeographic assessments also change accordingly.

Particularly since the advent of molecular techniques, avian systematics has been in a 'splitting' phase (Peterson 1998), and in the Amazon basin as in other regions, subspecies are frequently raised to species status, usually but not always along parapatric

distributional limits (e.g., Whitney et al. 2000, Isler et al. 2007a, Isler et al. 2007b). The recently increasing use of avian vocalizations in defining species limits has proven especially useful in this regard (Isler et al. 1998, Peterson 1998, Isler et al. 2007b).

Previously undescribed taxa are also still being found in the Amazon basin, usually with restricted distributions (Whitney and Alvarez 1998, Krabbe et al. 1999, Isler et al. 2001, Whittaker 2002, Whitney et al. 2004, Whitney and Alvarez 2005, Lane et al. 2007). In a few cases, poorly documented species long considered probable taxonomic anomalies have been rediscovered and their distributions more adequately documented (Gerhart 2004, Lane et al. 2006). The general biogeographic consequence in all these cases is an increase in apparent diversity. For example, when two conspecific subspecies separated by the Amazon River are raised to the status of separate species, communities on opposite sides of the river appear to become more different, thus causing an increase in beta diversity (defined here very broadly as taxonomic compositional difference among places). When a new species is discovered in a particular region, the local diversity appears to increase, and the area appears to become more biologically different from other areas (both alpha and beta diversity increase).

Systematics is also critical to historical biogeography. In order to know what events may have influenced speciation, we need to know when species radiations actually occurred. Most information regarding the ages of Amazonian bird species, particularly given the relative absence of a good fossil record, comes from recent progress in molecular phylogenetics. The field is still young, but most of this work has indicated that the Miocene and Pliocene were important periods of speciation in northern South

America (Klicka and Zink 1997, Roy et al. 1997, Da Silva and Patton 1998, Moritz et al. 2000, Glor et al. 2001, Lessa et al. 2003, Aleixo 2004), while the Pleistocene was important for subspecies-level diversifications and more limited cases of speciation (Cheviron et al. 2005, Ribas et al. 2006). This agrees with findings that South American biological diversity in general was likely comparable to modern diversity levels well before the Pleistocene (Wilf et al. 2003, Antoine et al. 2006). Many Andean bird taxa, however, may be exceptions to this general rule. Most South American species-level diversifications that have been attributed through molecular methods to the Pleistocene have occurred within Andean taxa, whereas Amazonian bird species appear to be much older on average (Fjeldsa 1994, Garcia-Moreno et al. 1999, Weir 2006, Price 2008). Even so, some Andean species once hypothesized to have originated during the late Pleistocene climatic shifts have been shown through molecular analyses to be somewhat older (Burns and Naoki 2004, Perez-Eman 2005).

It should be noted that most molecular work in dating speciation events has been based on molecular clock assumptions that have only been calibrated for a small number of species, typically not closely related to the species under consideration in any given study (Price 2008). Molecular clock assumptions have been the subject of ongoing debate (Peterson 2006), but a recent analysis of 90 avian taxa across 13 orders that compared sequence divergence in the mitochondrial cytochrome *b* gene to independently derived divergence dates based on fossils and well-documented biogeographic events found support for clocklike mutation rates over the past 12 million years, though there was minor variation among taxa (Weir and Schluter 2008). The general rule of two percent

sequence difference per one million years, which was also supported by Weir & Schluter's (2008) analysis, appears to be safe at least for the geologically recent past, and for estimating to within the nearest few million years—and this level of resolution is critical for interpreting Amazonian species-level diversifications. Clock-like mutation rates have conversely been refuted across a phylogenetically broad sample of 35 avian taxa (Pereira and Baker 2006), but that study examined diversification across much longer timescales (tens to hundreds of millions of years) and much deeper phylogenetic levels.

Historical causes of present-day diversity and distributions

Given what we know about the geologically recent history of the western Amazon, and the tempo and mode of speciation during that same time period, what can be said about the actual causes of speciation and the modern-day distributions of resultant bird diversity? While there appears to be widespread recognition that a disproportionately high number of speciation events occurred during the Miocene and Pliocene, the literature dealing with drivers of evolutionary change has largely remained focused on the Pleistocene. A major new research agenda opened up by recent progress in geologic and geomorphologic studies and molecular phylogenetic work is to relate diversification during the Miocene-Pliocene to its potential physical-environmental drivers. Did marine incursions divide the proto-Amazon basin into multiple large forest refugia (Nores 1999, 2004)? Did a shallow freshwater mega-lake create vast archipelagoes of forest fragments (Hoorn 2006b)? Have populations continuously become isolated along the lines of ever-

changing geologic conditions and their unique associated habitats? It remains to be seen whether or not modern Amazonian species distributions can be partly explained with geographically explicit reconstructions of the physical-environmental drivers of Miocene-Pliocene species radiations. An important lesson learned from the Pleistocene refugia debate (discussed in the Pleistocene section below) is that we should not expect any such explanations to rely on simple spatial associations of taxonomic distributions, because range shifts due to dispersal can easily obscure historical associations.

The question of whether or not species can diverge in sympatry or parapatry is important for the interpretation of historical events, because if spatial isolation (allopatry) of populations is not necessary for speciation, then the evolutionary importance of habitat heterogeneity changes drastically. For example, for sister taxa that segregate along the contemporary várzea-terra firme habitat transition, an evolutionary model that requires geographic isolation of populations forces us to search for evidence that either the historical analogues of those two habitats were geographically separated at some time in the past, or the habitat associations of the species involved have changed drastically since speciation. A model that allows for sympatric speciation along habitat gradients obviates those demands, but it does bring up the question of what kinds of habitat gradients existed during the time when speciation occurred. If the speciation event in question is sufficiently old, the task of reconstructing contemporary environments may be quite difficult.

Recent progress in evolutionary biology has shown sympatric evolution to be both theoretically possible and experimentally supported, and the view is taken here that it

should be taken into consideration in interpretations of Amazonian evolutionary history (Schluter 1996, Orr and Smith 1998, Losos and Glor 2003, Smith et al. 2005, Boul et al. 2007, Price 2008, Schluter 2009). However, most theoretical and empirical studies of avian speciation continue to support the genetic divergence of allopatric populations as the dominant, if not sole, means of diversification (Peterson et al. 1999, Price 2008). In general, models of historical diversifications should remain open to possibilities of allopatric, parapatric, and sympatric evolution, each of which may have been important for different taxa (Bates 2000). With these ideas in mind, we can review the events of the evolutionarily recent past.

Miocene-Pliocene

The period from about 23 to 2.5 million years ago (the Neogene) is chiefly marked by the ubiquitous influence of the Andean orogeny on the physical geography of the Amazon basin. Changes in landforms and hydrology that resulted from Andean uplift had potentially profound consequences for the evolution of Amazonian taxa for reasons beyond the physical barrier to dispersal that the new mountain chain presented. In addition to that important factor, erosional and depositional systems were redirected on a massive scale, creating new growth conditions for forest habitats across wide areas, and the series of hydrologic systems that eventually resulted in the modern Amazon river may have isolated terrestrial habitats from one another by long distances (Hoorn 2006b). These conditions may have been responsible for avian species radiations, whether by allopatric or sympatric mechanisms, or by both.

The region that is today western Amazonia was receiving sediments from the east prior to Andean orogeny, from the Brazilian and Guiana Shields, but as the Andes rose, sediments came increasingly from the new mountains themselves (Hoorn 1994, Hoorn et al. 1995, Hoorn and Vonhof 2006). Therefore, at the most general level, western Amazonian soils before the Andean orogeny may have been more quartzitic and poorer in nutrients than the younger, relatively nutrient-rich sediments that began covering vast areas of western Amazonia during the Andean uplift of the Miocene-Pliocene.

Fine et al. (2005) and Richardson et al. (2001) have given evidence that diversification in at least some dominant plant groups (Burseraceae and *Inga*, respectively) during the Miocene-Pliocene followed the geologic progression of changing edaphic conditions. That is, species adapted to relatively fertile clay soils are apparently more recently evolved than related species adapted to sandy, less fertile soils in the same region. This suggests that vast areas of western Amazonian bird habitat may be a relatively young habitat type (terra firme forest on clay soils), in terms of floristic composition. This also accords broadly with continental-scale studies of Amazonian forests that have found east-west gradients in floristics and structure (ter Steege et al. 2006).

Bates et al. (1998) suggested that some western Amazonian bird species may be recently derived from eastern relatives, and a taxonomically broad phylogenetic survey suggested that the pattern may be fairly general among avian taxa (Aleixo and Rossetti 2007). Silva and Oren (1996) suggested the same for primates, though they did not explicitly discuss habitat associations. A significant east-west trend in small mammal

species turnover was also found at a smaller spatial scale along the Juruá River in western Brazil, with the implication that speciation events have been related to the Andean orogeny (Gascon et al. 2000). Perhaps the most detailed descriptions of east-west phylogeographic patterns in birds have come from phylogenetic studies of parrot genera (Ribas et al. 2005, Ribas et al. 2009). The genera *Brotogeris* and *Pyrilia* both contain sister taxon pairs that have apparently diverged along an east-west boundary in the central Amazon. The divergence dates have been placed at the middle Pleistocene (about 1 mya) for the *Brotogeris* pair, and at the Late Miocene/Early Pliocene (about 5 mya) for the *Pyrilia* pair.

In terms of habitat associations, one would expect that western Amazonian bird species associated with nutrient-poor habitats such as white sand forests are closely related to species with more eastern distributions, and that many of the more widespread western Amazonian species associated with nutrient-rich habitats may be derived from one of those former groups. Support for this idea has come from avifaunal similarities between Peruvian white sand forests and the Guiana Shield (Whitney and Alvarez 1998, Alvarez and Whitney 2003). Some western Amazonian species may have evolved from eastern taxa as a result of the fragmentation and isolation of quartzitic-soil forest habitats containing remnant populations of the eastern taxa. As pointed out by Fine et al. (2005), it is important to consider the role of more recent habitat analogues in maintaining populations of much older taxa, because relatively nutrient-poor, sandy river-terrace formations as well as the Peruvian white sand forests of today may be Pleistocene Andean deposits on top of Miocene-Pliocene clay deposits (Räsänen et al. 1998). There

are also extensive sandy-soil formations in the western Amazon of late Miocene origin, overlaying middle Miocene clay deposits (Rebata et al. 2006). Their edaphic properties can resemble those of older eastern Amazonian formations, and their plant species compositions can be similar. This complicates interpretations of avian evolution, because western Amazonian specialists on nutrient-poor habitats could be close relatives of eastern taxa either because they were isolated in place during the Miocene-Pliocene as described above, or because eastern taxa more recently colonized newly formed nutrient-poor habitats in the western Amazon. Phylogenetic reconstructions of relevant taxonomic groups, with molecular clock dating of speciation events coupled to geomorphologic reconstructions, will be helpful for addressing these questions.

Terrestrial Miocene-Pliocene environments within the western Amazon itself must have varied greatly. If a shallow lacustrine-estuarine system dominated the region during the early to middle Miocene following rapid Andean uplift, vast landscapes may have been characterized by conditions not unlike today's várzea forests, palm swamps, and other inundated environments (Hoorn 1994). Deeper waters may have isolated islands, creating conditions for vicariance among terrestrial biota. Waters eventually receded when the incipient Amazon River began draining to the Atlantic Ocean (Hoorn 2006b). The specific consequences of this prolonged episode, the dating of which coincides broadly with a period thought to be of particular importance for Amazonian species-level diversifications, have not been investigated in detail for any avian group.

Sea incursions into the Amazon basin have also been proposed as mechanisms for allopatric speciation leading to present-day biogeographic patterns, with equivocal

support from various terrestrial taxa (Nores 1999). Debate exists concerning the extent and duration of marine incursions into the Amazon, but there is at least general agreement that episodic sea-level rise events during the early and middle Miocene were accompanied by incursions of some extent (Hoorn et al. 1995, Räsänen et al. 1995, Hoorn 1996, 2006b). Incursions in the western Amazon during the late Miocene (8 to 10 mya) may have reached as far south as the present-day location of the Amazon River (Rebata et al. 2006). These would certainly have isolated terrestrial environments from one another in some regions, particularly in northwestern Amazonia where a connection to the Caribbean probably formed.

Pleistocene

Any discussion of Amazonian biogeography would be incomplete without some discussion of the controversial and well-known Pleistocene refugia hypothesis that was first applied to the Amazon basin by Haffer (1969, 1974). Climate change is the defining feature of the Pleistocene, and glacial cycles clearly influenced Amazonian biogeography regardless of whether or not the refugia hypothesis is specifically correct. However, important geological processes that initiated with the Andean orogeny also continued during the Pleistocene. They include the deposition onto Miocene-Pliocene sediments of newer sediments with distinctive properties, and the continued development of várzea and other floodplain habitats associated with river-channel evolution.

Haffer argued, on the basis of a hypothesis that had been proposed for both temperate and tropical biota in other regions (Darlington 1957, Moreau 1966), that most

Amazonian bird species had diverged from parent species during the Pleistocene, when reductions in moisture levels during glacial periods led to the contraction of forest habitats into multiple, isolated patches surrounded by savannah. Multiple populations of a single widespread species would have been isolated from one another, making allopatric speciation possible (Mayr 1942, 1963). During wetter interglacial periods, forest advanced from these isolated refugia, carrying recently diverged populations with it, until those populations came back into secondary contact and either freely overlapped without interbreeding, competitively excluded one another from their respective ranges, or hybridized and lost their short-lived distinctiveness, depending on the level of differentiation that had been achieved during isolation. This process, extended over multiple glacial cycles, was proposed as a critical factor in the evolution of the high species diversity found in tropical lowlands (Haffer 1997).

The forest refugia hypothesis stimulated a great deal of biogeographic research in Amazonia and elsewhere, probably because it was appealing as a robust mechanism for the generation, rather than simply the maintenance, of tropical species diversity (Bush 1994). Bird species distributions were initially the primary evidence used to support the hypothesis (Haffer 1969, 1974), and subsequent research added plants, primates, butterflies, *Anolis* lizards, and other groups to the list of biota whose distributional patterns purportedly reflected the influence of Pleistocene refugia (works in Simpson and Haffer 1978, Prance 1982). It was also noted, however, that refugial patterns broadly coincided with patterns of present-day environmental differentiation, and that dispersal could nearly always be invoked to force unruly distributional data into desirable historical

patterns, so that distributional data in themselves did not constitute sufficient evidence (Endler 1982).

Early geomorphologic evidence for dry conditions during glacial periods, including sand dunes, areas with extremely sand-rich soils, and stone lines in soil strata (e.g., Haffer 1969, Ab'Saber 1982) have largely been shown to have plausible alternative explanations (Bush 1994, Colinvaux et al. 2000). Early palynological evidence appeared to support the idea that most of Amazonia had become savannah during glacial periods (Van der Hammen 1974, Absy and Van der Hammen 1976), but the addition of more sites with palynological records has indicated that, at best, only minor portions of the basin experienced this change (Colinvaux 1987, Bush and Colinvaux 1988, Colinvaux 1997, Hooghiemstra and Van der Hammen 1998, Haberle and Maslin 1999, Colinvaux et al. 2000).

Additional evidence has suggested that high-altitude floristic elements moved into Amazonian lowlands as a response to lowered temperatures rather than increased aridity during glacial periods, particularly in hypothetical refugial areas. Those floristic changes, even under the hypothesis that forest cover remained continuous throughout Amazonia, have been proposed as a sufficient mechanism for the periodic isolation of allopatric populations (Bush 1994, Colinvaux 1998, Bush et al. 2004). Widely divergent interpretations of palynological evidence have therefore resulted in similar interpretations of the effect of climatic changes on speciation patterns. This demonstrates that controversy concerning the relationship between current species distributions and

climate-driven speciation during the Pleistocene may not be settled with palynological data alone.

An additional problem concerning the correlation between species distribution patterns and historical habitat distributions has been the incompleteness of distributional data in the Amazon basin. Although most species distributions may be largely correct as currently described, recent modifications of the range maps of many species suggest that mistakes can easily be made by assuming that distributions are fully known. The recent elucidation of the distributions of two *Leucopternis* hawks serves as an example. *Leucopternis kuhli* and *L. melanops*, which are sister taxa (Amaral et al. 2006), were thought until quite recently to have been wholly allopatric, with *L. melanops* restricted to forests north of the Amazon River, and *L. kuhli* south of the river. This species pair thus could be interpreted as supporting a refugial speciation hypothesis. However, it is now known that *L. melanops* occurs widely in the Amazon basin south of the Amazon River, where the two species are sympatric (Amaral et al. 2007). Leucopternis *melanops* was overlooked due to the similar appearance of the two taxa, and to insufficient sampling in the sandy-soil terra firme habitats to which the species may be restricted in the southern part of its range. In fact, the extent of its distribution is still not fully known (Amaral et al. 2007).

Perhaps the most convincing evidence both for and against Pleistocene evolutionary diversifications comes from molecular phylogenetic analyses of the organisms involved, since these attempt to provide direct indications of the age of speciation events (Moritz et al. 2000). Most molecular work has indicated that species are

generally older than Pleistocene glacial events, but that many subspecific diversifications may have Pleistocene origins; evidence for increased speciation rates during the Pleistocene has not been found (Klicka and Zink 1997, Da Silva and Patton 1998, Moritz et al. 2000, Glor et al. 2001, Lessa et al. 2003, Aleixo 2004, Zink et al. 2004, Weir 2006).

Nonetheless, climatic variability cannot be ruled out as an important factor in speciation during the late Tertiary (Klicka and Zink 1997). The refugia hypothesis is a variant of the much more general concept of allopatric speciation by vicariance (Price 2008), and it is not fundamentally different in that regard from several competing ideas, such as the riverine barrier and Miocene marine incursion hypotheses. Forest refugia were appealing at a time when allopatry was considered by most evolutionary biologists to be necessary for speciation, and this underlying assumption drives interest in all vicariance models. However, it has been increasingly recognized that ecological differentiation along environmental gradients, or even in complete sympatry, can be sufficient for reproductive isolation (Schluter 1996, Orr and Smith 1998, Losos and Glor 2003, Smith et al. 2005, Price 2008). While vicariance models will continue to be important for explaining Amazonian diversifications, an undue emphasis on vicariance should not be allowed to overshadow sympatric and parapatric speciation models. All three models have probably contributed to Amazonian diversity, and the generality of any single model such as the Pleistocene refugia hypothesis will therefore be limited, even if it is correct for some taxa.

It is possible that the most important biogeographic changes to occur during the Pleistocene were associated not with speciation, but with the dispersal of existing taxa. It

is reasonable to assume that geomorphologic and climatic developments during the Pleistocene were sufficient to significantly reorganize habitat distributions and to generate new habitats and extinguish old ones, notwithstanding the uncertainty surrounding the specific character of those changes in many cases. Isolated sandy-soil formations have been created in the western Amazon as a result of the erosion and deposition of material during the Pleistocene (Räsänen et al. 1998, Rebata et al. 2006). It is also reasonable to assume that avian taxa were capable of responding to those changes through significant range shifts.

Holocene (~12,000 years ago to present)

Significant genetic diversification at the subspecies or species level has probably occurred in very few Amazonian bird species during the Holocene, so that changes in biogeographic diversity have been due instead to changes in the distributions and abundances of existing taxa. Given the rapid rates at which bird populations are capable of colonizing new areas where habitat conditions become favorable, those changes have probably been widespread and considerable. Changes in the distributions of habitats have likely resulted from minor climatic variations since the most recent (Wisconsin) glacial period (Haberle and Maslin 1999), and from erosional and depositional processes that have in particular re-worked river floodplains. In the western Amazon, sandy-soil terrace formations have been deposited to form non-flooded uplands during the Pleistocene and into the Holocene, creating soil type heterogeneity in large areas adjacent to river floodplains (Räsänen et al. 1998, Fine et al. 2005). In some cases, animal populations that

were formerly on one side of a major river may have been 'moved' to the opposite side by a river channel cut-off, which could have significant genetic consequences if the river channel otherwise limits dispersal (Peres et al. 1996).

The most significant habitat alterations during the Holocene, however, have probably been anthropogenic. First arrival times of human populations to various parts of the Amazon are highly uncertain, but significant areas were probably populated several thousand years ago, and populations were quite dense along the main stem of the Amazon and major tributaries by the time Francisco de Orellana made his exploratory voyage in 1542 (Denevan 1992, Mann 2005). Humanized habitats have thus had a long-term presence in the Amazon basin, but have become far more widespread in recent years. The largest and most desirable timber trees have been removed from very large portions of Amazonian forests, and abundances of many of the largest aquatic and terrestrial wildlife species have been reduced through hunting. These and other human activities have altered habitats even where forest and other natural habitats largely remain. Stronger effects have occurred in areas that have been largely deforested, particularly along the major eastern and southern Amazonian deforestation fronts in Brazil. These and other anthropogenic effects are discussed in more detail below.

DISPERSAL LIMITATION

Dispersal limitation has been postulated as an important factor maintaining community diversity, notably in island biogeography theory (Brown and Kodric-Brown 1977) and

metapopulation dynamics (Hanski and Gilpin 1991). Its effect is somewhat intuitive: high dispersal rates between two areas should translate to high compositional similarity, because species which at first are present in only one area are likely to colonize the other area through dispersal. Dispersal limitation between two areas should have the opposite effect (Nekola and White 1999). So-called neutral theory (Hubbell 1997, Hubbell 2001) formalizes this relationship, explicitly isolating the effect of dispersal limitation from ecological effects by treating all species as if they were ecologically identical, and therefore competitively equal. Neutral theory as applied to biodiversity and biogeography develops the principle of ecological drift, which is directly analogous to, and based upon, the theory of genetic drift. The potential applications in biogeography of the ecological drift concept are very broad, and only the specific component dealing with the relationship between dispersal limitation and beta-diversity is summarized here.

Dispersal limitation can also be caused, of course, by geographic features that present clear physical obstacles. In the Western Amazon, the clearest such feature is the Andes mountain chain, which bounds the entire region to the west. A more subtle feature, but one whose relevance for avian biogeography has been well-documented, is the Amazon River itself, as well as some of its largest tributaries.

Neutral theory

Neutral theory is framed in a metacommunity context, where a single community is defined as a group of individuals occupying an area within which the likelihood of dispersal of any of the individuals to any site is equally likely; i.e., there is no dispersal

limitation (Hubbell 2001). The metacommunity, then, is the set of all such communities under consideration in a wider area. Metacommunity structure may be easiest to conceptualize as a set of spatially distinct communities, but the neutral theory applies equally to the case of contiguous, homogeneous space. In this case, a local community is that group of individuals around a central location for whom dispersal to that location is not limited. Dispersal limitation therefore only affects migration among communities.

Neutral theory assumes a fixed number of individuals for a given community, where individuals die and are replaced randomly by dispersal of a new individual. Considering only within-community dispersal, the likelihood that the new individual is of a given species is directly proportional to the abundance of that species; i.e., ecological differences among species are ignored. The likelihood that a dying individual will be replaced by a species from a different community depends on both the abundance of the species and the likelihood of dispersal, which is a function of distance. If distant communities contain some species not currently represented in the community of interest, then there is some likelihood that the new individual will also represent a new species in the community. This means that, as dispersal limitation is removed, the species composition of a given community is increasingly similar to the total species pool in the metacommunity. As dispersal limitation increases, replacement individuals are increasingly drawn from the local community, and therefore from a lower number of species. Species that are more common are more likely to contribute new individuals, so they tend to increase their dominance, whereas rare species tend to become more rare. Dispersal limitation therefore makes individual communities less speciose (alpha-

diversity decreases), but communities also become less similar to one another (beta-diversity increases).

Dispersal limitation dictates that the chance of successful dispersal between communities decreases with increasing distance, so neutral theory predicts decreasing similarity of communities with increasing distance. Because neutral theory suggests that spatial variability in species assemblages will be generated through dispersal limitation even in the absence of ecological interactions among species or between species and their environments, geographic distance may itself be an important driver of biogeographic diversity, independently from historical and ecological factors (Hubbell 1997, Nekola and White 1999, Condit et al. 2002, Ruokolainen and Tuomisto 2002).

Amazonian rivers as boundaries

> During my residence in the Amazon district I took every opportunity of determining the limits of species, and I soon found that the Amazon, the Rio Negro and the Madeira formed the limits beyond which certain species never passed. The native hunters are perfectly acquainted with this fact, and always cross over the river when they want to procure particular animals, which are found even on the river's bank on one side, but never by any chance on the other.
>
> Alfred Russel Wallace (1852)

Ever since Wallace, the idea that rivers define important limits for birds, primates, and other taxa has been central to Amazonian biogeography. However, the mechanisms whereby differences between opposite banks of large rivers have been generated and maintained have remained quite uncertain. Indeed, even the reality of the differences has been questioned in many cases, leading to refinements in our understanding of the

complexity of the river boundary effect, including its taxonomic and geographic specificities.

Most Amazonian rivers, because they are small, are not likely to be concordant with distributional limits for most taxa, whereas several of the largest Amazonian rivers clearly are important sites of taxonomic disjunction. This river size effect may also act along the length of a single river—the Amazon River itself defines distributional limits for an increasing number of bird species as it grows wider toward its most downstream reaches (Hayes and Sewlal 2004).

Rivers have been proposed as mechanisms for allopatric speciation leading to present-day biogeographic patterns, with equivocal support from various taxa (Da Silva and Patton 1998, Gascon et al. 2000, Aleixo 2004, Nores 2004, Lovejoy et al. 2006). The widest rivers in the Amazon basin, it is argued, are a significant barrier to dispersal for many species, suggesting that populations on opposite riverbanks became genetically isolated either after vicariance due to river formation within original species ranges, or after dispersal across the river by a small colonizing population. More commonly, though, rivers are thought of not as original mechanisms of speciation, but merely as locations of secondary contact after allopatric speciation with subsequent dispersal. This model was supported by Haffer (1969) and multiple additional proponents of the Pleistocene refugia hypothesis, and it can potentially be deployed to explain riverine distributional limits under any allopatric speciation model, including those that propose isolation due to Miocene marine incursions or freshwater seas or wetland complexes in the western Amazon (e.g., Hoorn 2006b). In the latter contexts, the Pleistocene may be

seen as important not so much as a period of Amazonian species radiations, but as a period of rearrangement of species distributions, leading eventually to present-day biogeographic patterns including riverine distributional limits.

There is a competing hypothesis that rivers often demarcate limits of geomorphologic units in Amazonia, so that those units themselves, rather than dispersal limitation, may be responsible for species differences across rivers (Rossetti et al. 2005). This model of speciation across environmental gradients is similar to Endler's (1982) early critique of the Pleistocene refugia hypothesis. Under a hypothesis of parapatric speciation across environmental boundaries at Amazonian rivers, we should expect to see close correlation between bird and plant species turnover across major rivers. Plants especially should be affected by differences between geomorphologic formations, because they are directly influenced by geologic and hydrologic abiotic conditions. Bird species turnover among formations would then be expected to follow from plant species turnover and associated environmental differences.

There is currently no single hypothesis, or set of hypotheses, which satisfactorily explains continental-scale Amazonian avian biogeographic patterns in terms of historical conditions and processes or in terms of present-day environments. Whatever their cause, definable biogeographic zones appear to exist among a significant portion of avian taxa, and their boundaries are in some important cases coterminous with major rivers (Peters 1931-1987, Haffer 1974, Beven et al. 1984, Schulenberg et al. 2007, Burney and Brumfield 2009, Ridgely and Tudor 2009). These zones are often defined by congeneric species replacements or conspecific subspecies replacements, so by definition, they refer

to some combination of historical evolutionary diversifications and more recent range shifts. While recent phylogeographic analyses have enhanced our understanding of evolutionary relationships among the taxa occupying different Amazonian regions at continental scales, much less attention has been paid to the mechanisms that maintain present-day regional distinctiveness, which is fundamentally a question of dispersal limitation, broadly defined. Questions of particular interest are whether or not environmental differences among zones, and other factors described below, can explain biological distinctiveness among zones without the need to invoke additional historical explanations; and if not, how substantially historical factors have affected modern biogeographic diversity.

ECOLOGY AND ENVIRONMENT

Niche and habitat

One of the most basic ecological principles underlying explanations of biogeographic patterns is the niche. According to niche theory, a species has a particular set of environmental requirements for the completion of its life cycle, so that the spatial distribution of the species is limited by that of its requisite habitat (Grinnell 1916, Hutchinson 1957). If all species respond individually to their own habitat requirements in this way, then the total species assemblage at a particular place may be seen as the result of spatial overlap, or lack thereof, among the niches of all species (Gleason 1939, Whittaker 1978). Of course, species in the same landscapes constitute active, dynamic

components of one another's habitat, and interactions among community members can strongly influence the distributions of populations. Habitat occupancies that are limited by features of the physical environment on one hand, and by the social or community environment on the other hand, have been associated with the fundamental niche and the realized niche, respectively (Hutchinson 1957, Pearman et al. 2008).

When there is a high degree of coincidence among the habitat distributions of many species, particular species assemblages may recur in many places. Recurring assemblages of this kind may be interpreted as identifiable biological community types, but they are conceptually distinct from the successional and climax communities described by Clements (1936), because no endogenous organizational principle need be invoked—they can be seen simply as the product of underlying habitat distributions, interpreted at the level of the individual species.

Alternatively, the niche of each species may be sufficiently distinctive from all others, and interactions among species sufficiently weak, that community types do not recur across landscapes, and typological classification schemes are not useful (Whittaker 1975, Brown and Lomolino 1998). In either case, change in species composition may be abrupt or gradual, depending upon the gain and loss of species across abrupt or gradual habitat gradients (Whittaker 1967). Regardless of whether or not community types can be identified, environmental conditions are important determinants of which species occur in a given location, so a correlation should be observable between geographic variation in environments and in communities. Observing such a correlation depends, of course, on

having correctly identified environmental variables that are important with respect to the niches of the species involved.

Many Amazonian bird species do show very restrictive habitat affinities (Terborgh et al. 1990, Robinson and Terborgh 1997, Whitney and Alvarez 1998, Alvarez and Whitney 2003). Local species diversity has been correlated with the diversity of habitat types present, as should be expected if species have variable abundances among habitat types (Terborgh et al. 1990, Cohn-Haft et al. 1997, Aleixo et al. 2000). Readily recognizable habitat types that often occur in closely intermixed patches such as terra firme forest, flooded (ígapo and várzea) forests, palm swamps, disturbed riparian vegetation, secondary forests and agricultural clearings are widely distributed across the Amazon basin, and contribute to community heterogeneity to greater or lesser degrees in most areas. Related taxa often segregate spatially by these habitat types, which have probably therefore been important for evolutionary diversifications (Remsen and Parker 1983, Aleixo 2002, Alvarez and Whitney 2003). The distinction between floodplain forests and terra firme forests is one of the most fundamental, with many bird species largely restricted to one or the other, and it has been estimated that about 17 percent of the western Amazon lies within river floodplains, most of it forested (Toivonen et al. 2007). Lovejoy (1975) documented differences in bird communities between flooded (várzea and ígapo) and non-flooded (terra firme) forests near the mouth of the Amazon in eastern Brazil, concluding that the most pronounced differences were shown by uncommon species, with common species tending to occur in both habitats.

Less visible habitat type variations that have not been as thoroughly characterized exist within the Amazon basin and may be of equal importance to wildlife distributions, particularly among terra firme areas with different fluvial histories and soil properties (Tuomisto et al. 1995, Räsänen et al. 1998, Whitney and Alvarez 1998). Terra firme forests are far more extensive than river floodplain-associated habitats, but far less accessible. Sampling efforts have therefore not historically favored the adequate description of terra firme forest types (Terborgh 1985, Tuomisto and Ruokolainen 1997), and the specific habitat affinities of many terra firme bird species are largely unknown. Vegetation broadly typical of western Amazonian terra firme forests is shown in Photos 1.1 through 1.4.

Comparisons of avian communities among a few widely separated terra firme sites in the Amazon basin have demonstrated high variability in composition and in the relative abundances of shared species, but the likely role of environmental variability in generating community differences has not been assessed (Karr et al. 1990, Stouffer 2007). Descriptions of distinctive bird communities in terra firme areas dominated by white sand soils, however, show that strong within-terra firme habitat affinities do exist. Alvarez (2002) and Alvarez and Whitney (2003) documented important differences between white sand forests and other terra firme forests on more nutrient-rich soils in the Peruvian Amazon, and Borges (2004) documented unique bird communities in similar, but more open, habitats (*campinas* and *campinaranas*) associated with sandy soils further

Photo 1.1. Typical canopy of a mature, terra firme forest in Loreto, Peru. Notice both the strong heterogeneity in individual tree physiognomy (as well as phenology) and the unevenness of general canopy arrangement.

Photo 1.2. Typical midstory of mature, terra firme forest in Loreto, Peru.

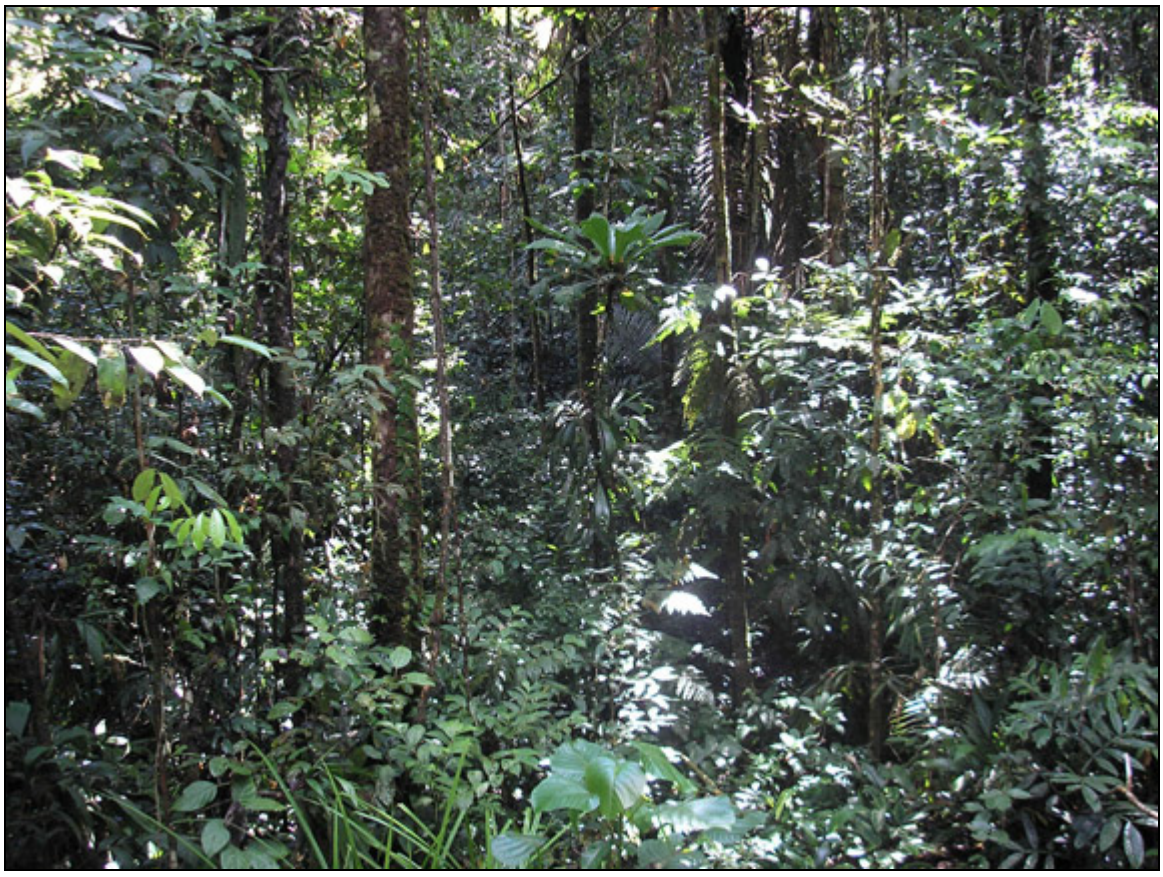


Photo 1.3. Relatively dense understory and midstory of mature, terra firme forest in Loreto, Peru.

Photo 1.4. The spatial structure of mature forest understory is highly variable. In this case, a dense stand of understory palms and small trees in the background gives way to a very open area with a few small palms in the foreground.

east in Brazil. A general texture and nutrient gradient can be seen between sandy, nutrient-poor soils and more clayey, nutrient-rich soils in the Amazon basin, and variations in forest structure and floristic composition are associated with this gradient (Photos 1.5 – 1.8; see following section for a detailed discussion). The predominant geomorphologic formations in the western Amazon are associated with clayey soils (Hoorn 1994, 1996, Rebata et al. 2006), whereas white sand soils represent both a sandy, nutrient-poor edaphic extreme, and a geomorphologic phenomenon with very limited spatial extent (Räsänen et al. 1998). Other sandy-soil formations that occupy less extreme positions along edaphic gradients are more extensive in the western Amazon, including relatively broad terra firme areas such as the Nauta formation (Räsänen et al. 1998, Rebata et al. 2006) as well as the so-called brown sand terra firme, river terrace formations broadly bordering major rivers (Räsänen et al. 1998, Fine et al. 2005). Edaphic variation that leads to forest floristic and structural variation should therefore be considered an important focus of investigations that seek to explain spatial variation in bird populations and communities. Peres (2000b) demonstrated a correlation between soil fertility and the abundances of several large, hunted bird species in the western Brazilian Amazon, and the effect remained important even when independent effects of hunting pressure were accounted for. Arbeláez et al. (2008) found that edaphic variation among terra firme locations in the Colombian Amazon exerted a strong influence on the composition and productivity of fish communities in forest streams.

Photo 1.5. Typical understory and midstory of mature, terra firme forest in Loreto, Peru. Understory palms shown here are normally indicative of relatively nutrient-rich soil conditions, and were common at most of the nutrient-rich sites included in this study.

Photo 1.6. Midstory and canopy of *varillal* terra firme forest on white-sand soils in the Allpahuayo-Mishana National Reserve near Iquitos, Peru.

Photo 1.7. Streams in clay-soil terra firme forests are normally browner and more opaque (referred to, ironically, as 'white water') than those in sandy-soil forests, due to higher sediment loads. The cohesive properties of clay also often result in more vertically eroded banks, such as the one shown here.

Photo 1.8. Streams in sandy-soil terra firme forests are normally clearer than those in clayey-soil forests due to lower sediment loads, but are darkly tinted, reminiscent of tea, due to high concentrations of tannins leached from vegetation. A large deposit of fine sand occupies the far bank shown here.

Unfortunately, few studies have attempted to correlate compositional change in Amazonian bird communities over time or space with any quantitative measure of a specific environmental variable, except when anthropogenic habitat alterations have been the variables of interest (see below). Generalized habitat types, defined qualitatively, have instead formed the units of comparison. In non-Amazonian regions, numerous environmental variables, typically representing vegetation characteristics, have been shown to be associated with bird community composition at various spatial and temporal scales (e.g., Rotenberry 1985, King et al. 2000, Githaiga-Mwicigi et al. 2002, MacNally et al. 2002, Robinson et al. 2004, Lee and Rotenberry 2005, Fleishman and MacNally 2006, Jayapal et al. 2009), and there is good reason to assume that Amazonian bird communities are also strongly influenced by multiple non-anthropogenic, measurable environmental factors at multiple scales.

Insects are a primary food source for birds, and it can be expected that spatial and temporal variation in insect abundance and species composition may influence avian community composition. The work required to test this idea has not been done in any Amazonian region, and very little is known about the nature of insect beta diversity in the Amazon basin, or in the other major tropical lowland forest regions. Sääksjärvi et al. (2006) found evidence for a positive relationship between plant and parasitoid wasp species richness in the Peruvian Amazon, and an association between variation in plant species and wasp species composition. However, differences among sites in wasp composition were small in relation to the strong differences in plant composition. Recent work in Papua New Guinea suggests that herbivorous insect beta diversity may be quite

low in the lowlands, even across very large distances (Novotny et al. 2007). Much important work in the western Amazon remains to be done in this area. In particular, tree species that are specialized on different soil types have evolved different levels of defensive chemical compounds to protect against herbivory by insects (Fine et al. 2004, Fine et al. 2005), whereby lower soil nutrient levels and slower tree growth rates are associated with higher levels of defensive compounds. There is reason to suspect that different insect species have in turn evolved specializations on plant food sources with qualitatively or quantitatively different defensive compounds, and analogous specializations may exist at higher trophic levels, i.e., birds and other insectivorous predators.

Forest floristics and structure

Amazonian botanical studies have been more productive in this regard. This literature is crucial to Amazonian bird habitat studies because of the direct and indirect dependence of birds on vegetation for the completion of nearly all aspects of their life history. Gentry (1988) reported a high degree of plant community differentiation in Amazonia, in terms of both species richness and composition, related to edaphic properties (soil nutrients and texture) and precipitation. Other researchers have subsequently demonstrated similar responses to edaphic conditions by particular taxonomic or physiognomic plant groups. Pteridophytes (ferns and allies) and Melastomataceae have been particularly well-examined (Young and León 1989, Tuomisto and Ruokolainen 1994, Ruokolainen et al. 1997, Tuomisto et al. 2002, Tuomisto et al. 2003a, Tuomisto et al. 2003b); Burseraceae

(Fine et al. 2004, 2005) and trees in general (Ruokolainen et al. 1997, Phillips et al. 2003) have shown similar responses to edaphic conditions. Comparisons of tree (Terborgh and Andresen 1998) and liana (Burnham 2002) communities between seasonally flooded and non-flooded forests have suggested that differences are present, but slight in comparison to the apparent differences in physiological stress imposed by flooding. Topography has also been found to contribute partially to community differences for trees, pteridophytes, and Melastomes (Tuomisto et al. 1995, Tuomisto et al. 2003b, Valencia et al. 2004).

Vegetation characteristics are among the most important environmental features for birds, and variability in Amazonian plant communities should be expected to affect bird species composition. It is important in this regard to distinguish between plant taxonomic composition (floristics) and the physical structure (physiognomy) of vegetation, which, while often spatially correlated, can affect bird communities differently (Rotenberry 1985, Gillespie and Walter 2001, Fleishman et al. 2003, Jayapal et al. 2009). Some Amazonian bird species with fairly specific habitat requirements are known to be associated with different plant species groups in different regions, as long as habitat structure requirements are met (Terborgh 1985). For example, several species thought to have been highly restricted to *Guadua* bamboo thickets in southern Peru have been located in structurally similar, but floristically entirely different, non-bamboo thickets in southeastern Amazonia (Aleixo et al. 2000). Both floristics and physiognomy influence bird communities, by affecting different species in different ways, sometimes at different scales (Rotenberry 1985). Understanding the influences of these factors independently of one another has important implications for the inference of wildlife

distributions from satellite imagery and from botanical survey, each of which represents floristic and physiognomic information in different ways (Tuomisto et al. 1994, Higgins and Ruokolainen 2004). Among studies that have investigated the role of habitat variability in structuring Amazonian bird communities, virtually none have attempted to disambiguate the roles of vegetation floristics and physiognomy.

A lone, early attempt to describe relationships between bird and plant community compositions was made by Lovejoy (1975), who examined large (> 10 cm diameter) tree species composition to bird species composition across a flooded to non-flooded forest gradient near the mouth of the Amazon River. Lovejoy did find a limited degree of correspondence between species turnover in the two groups, but site distinctiveness was more pronounced for trees than for birds. Some sites in the two different habitats shared nearly no tree species, while the most abundant bird species tended to be found at all sites. Lovejoy's interpretation was that trees responded directly to the edaphic and hydrologic variables that ultimately drove site differences, whereas birds were trophically separated from those factors, responding instead to variability in plant and insect communities. The notion that components of beta diversity which are fundamentally driven by abiotic factors decrease in strength with increasing trophic distance from those factors needs further testing. Specifically in the western Amazon, while edaphic and floristic variables can be expected to co-vary, floristic variables may be expected to have higher explanatory value than edaphic variables for bird community variation.

Local variation in habitat structure, particularly vegetation structure, has been an important component of avian habitat selection and community diversity studies at least

since the classic work done by MacArthur and others (MacArthur 1958, 1964, MacArthur et al. 1966), and early work on the influence of local variations of vegetation physiognomy on western Amazonian bird communities was done by Pearson (1974). These early studies tended to focus on species diversity and biomass, finding that in general, both increase with increasing structural complexity of habitats. Several early Amazonian studies attempted to correlate a foliage diversity index to bird species diversity, failing to find any such relationship (Terborgh and Weske 1969, Pearson 1974, Lovejoy 1975). None of those researchers concluded that structural complexity was unrelated to species diversity; rather, they concluded that foliage diversity indices are insufficient measures of structural complexity in tropical forests, where major structural components contributed by lianas, epiphytes and trees such as palms with atypical growth forms cannot be captured with simple indices.

Treefall gaps constitute a highly visible component of Amazonian forest structural diversity at the scale of the local tree stand (Photos 1.9 – 1.11). All areas of mature forest eventually experience gap formation due to wind, tree diseases, or other factors, and numerous bird species are specialized to some degree on the early phases of gap disturbance (Terborgh 1985, Wunderle et al. 2005, Wunderle et al. 2006). The effects of anthropogenic forest clearing have been much better studied than have treefall gaps or other natural forms of forest stand heterogeneity; forest clearing, fragmentation, and other structural changes due to human activities are discussed below.

Photo 1.9. Large trees such as this one create light gaps in the forest canopy when they fall, usually damaging or felling additional trees and branches in the process. The resulting tangle of densely piled live and dead vegetation is a habitat used by a number of forest bird species. Most of the 1 km transects used in this study passed through several such light gaps, in various stages of regeneration.

Photo 1.10. This large light gap in a mature forest, probably created by several falling trees during one or more windstorms, has begun to fill in with early successional tree species, including those in the genus *Cecropia*. Many forest bird species are associated with these early successional habitats. Eventually, longer-lived canopy species will overtake the shorter-statured *Cecropias*.

Photo 1.11. This extremely large light gap was opened by an unusually strong windstorm in September 2005 near the Nanay River in Loreto, Peru. Scattered small trees remain standing in the clearing, but the mature forest edge in the background is more than 150 m away. Such events are rare, and their effects on wildlife distributions and abundances are not well studied.

Landscape ecology

Avian species composition in one habitat can depend not only on that habitat's internal characteristics, but also on the proximity of other habitats and the configuration of different habitat patches relative to one another within a landscape (Holt 1993, Wiens 1995, Sisk 1997, Saab 1999, Wiens 1999). Primary forest canopy, for example, can be used heavily by species that nest and roost in open habitats such as river islands and large palm swamps, but forage more widely in surrounding areas. Amazonian forest canopy can also be used by species that are primarily associated with open habitats and forest edges (Naka 2004). Thus, the species composition of terra firme forests near large river floodplains or heavily farmed areas, for example, may be substantially different from that of more 'interior' terra firme, further away from floodplains or cleared areas. This influence may extend to quite large distances, given the daily foraging migrations of groups such as parrots and oropendolas. Landscape ecology principles also potentially apply to interactions between humans and forest wildlife, since such interactions are conditioned by the geographical relationships between settlements, forests, and access routes (Peres and Lake 2003, Parry et al. 2009). Some of these relationships are discussed below.

Pearman (2002) conducted one of the few investigations of the influence of landscape composition on Amazonian bird communities in which measures of forest vegetation structure and land cover were compared to community richness and composition. He used satellite imagery in eastern Ecuador to measure the amount of primary forest and anthropogenically cleared areas surrounding mist-net sites at multiple

spatial scales, and found that different avian guilds responded to different factors at different spatial scales. Understory insectivores were found to occur at lower densities in primary forests with deforested areas surrounding them, even when local vegetation structure was not noticeably affected; including wider areas around the capture sites strengthened the correlation. Thus, some species appear to be affected by broad-scale landscape factors that may influence dispersal, home range sizes, or other factors independently of more local habitat requirements. Such effects might be expected to be strong for some canopy species such as large frugivores with long daily foraging migrations, or smaller species for which canopy structure and light conditions may be similar to forest edges, but mist-net based survey methods will not be sufficient for studying canopy species.

HUMAN PROCESSES

Human activities influence the composition of wildlife communities directly and indirectly through habitat loss, habitat fragmentation, the creation of novel anthropogenic habitats, the introduction of invasive and exotic species, the introduction of toxins, anthropogenic climate change, hunting, and other processes (Groom 2006). I focus here on a few specific factors that affect bird communities within relatively unfragmented forests near human settlements, because standing forests that are used and altered by people are much more common than deforested land in the western Amazon.

The relatively small-scale and patchy deforestation of the western Amazon, while significant, contrasts strongly with the primary deforestation fronts in Brazil, where enormous areas of eastern and southern Amazonian forest have been cleared. By some estimates, approximately 15 percent of Brazilian Amazonian mature forest has been cleared, and equal or greater areas of existing forest may be affected in some way by fragmentation (Laurance et al. 2005). Accordingly, most studies of the effects of forest clearing and fragmentation have taken place in the Brazilian Amazon. These effects have possibly been the best-studied components of avian ecology in the Amazon basin, due to concern among conservation biologists over their negative impact on bird populations. The most well-known and complete study of fragmentation effects has been the Biological Dynamics of Forest Fragments Project in the central Brazilian Amazon (Bierregaard et al. 2001, Ferraz et al. 2007). Forest fragmentation has generally been associated with decreased species richness, the reduction or loss of populations of forest interior species particularly including understory insectivores, and the introduction or increased frequency of forest edge species inside fragmented forests (Pearman 2002, Barlow et al. 2006, Stouffer et al. 2006).

Forest conversion in the western Amazon consists primarily of clearing around rivers for small-scale agriculture, with additional clearing around the very few roads in the region (Romero and Ortiz 1998, Mäki 2003). Settlements occur near rivers because they are the primary means of transport, and in places where settlement density is relatively high, large contiguous tracts can exist as a patchwork of agricultural fields in various stages of use or secondary forest regeneration (Pacheco et al. 1998, Romero and

Ortiz 1998, Pearman 2002). Secondary forests near villages are often actively managed agroforests, despite their unkempt appearance (Padoch and Pinedo-Vasquez 2006). Such areas constitute a distinctive wildlife habitat, and contain a different set of wild species than adjacent forests (Andrade and Rubio-Torgler 1994, Aleixo 1999, Borges and Stouffer 1999, Naughton-Treves 2002, Naughton-Treves et al. 2003, Woltmann 2003).

In forests near agricultural areas, bird species assemblages may be subsidized with species primarily found in agricultural and edge habitats; this may be particularly true for natural forest openings such as large treefall gaps, and for the forest canopy, components of which can resemble edge habitats (Naka 2004). Compositional change can also result from the loss of forest interior species in fragmented forest, with understory insectivores tending to be the most vulnerable (Pearman 2002, Laurance 2004, 2006). Road clearing edges examined by Laurance (2004, 2006) in the Brazilian Amazon may have represented fragmentation patterns similar to those found along roads and rivers in the western Amazon. In that study, bird species richness and abundance were generally reduced with increasing proximity to road edges, with insectivores showing the strongest effects. Photos 1.12 – 1.21 show agricultural landscapes typical of the Peruvian Amazon, forest edges associated with them, and examples of typical forest extractive activities that can further modify fragmented forests.

People also influence bird species abundances directly through hunting and collecting for the pet trade. Commonly hunted terra-firme game birds in the western Amazon basin include large-bodied members of the families Tinamidae, Odontophoridae, Cracidae, and Psophiidae (Peres 2000b, Peres and Lake 2003). Photos 1.22 – 1.25 depict

Photo 1.12. This recently cleared *chacra* has been planted with maize and yuca, and is completely surrounded by young, regenerating secondary forest (*purma*). This *chacra-purma* landscape mosaic constitutes the primary form of mature forest clearing in central Loreto, and occurs chiefly along rivers, where *ribereño* communities are located. While commercial (and often illegal) logging probably represents a greater threat to wildlife diversity and abundance, it is often concentrated selectively on the largest forest trees and therefore does not necessarily result in obviously cleared landscapes such as this one.

Photo 1.13. Most forest fragmentation in central Loreto is a result of small-scale agriculture. This field had been very recently burned to clear vegetation, about a year after the trees were felled. Notice the young cassava (yuca) plants, which had been planted about a month before the photo was taken.

Photo 1.14. This man was helping to fell trees in a few hectares of secondary forest (*purma*) as a stage in the re-establishment of a new agricultural field (*chacra*), near the Tamshiyacu River in Loreto. This project was undertaken entirely with hand tools such as the axe that the man is holding, although chainsaws are sometimes available for use. *Chacras* are often created in older *purmas*, rather than in mature forest, partly because of the ease of clearing and proximity to the household. The repeated clearing of regenerating forest is not undertaken as a forest conservation measure, but it does incidentally reduce rates of mature forest clearing.

Photo 1.15. This woman was helping to clear a few hectares of secondary forest (*purma*) as a stage in the re-establishment of a new agricultural field (*chacra*), near the Tamshiyacu River in Loreto. The edge between the newly cleared area and older *purma* can be clearly seen. A similarly dramatic edge between *purma* and mature forest could be seen about 3 km away from the river edge. Purma occurs extensively along many rivers near Iquitos, creating a buffered transition between mature forest and cleared landscapes.

Photo 1.16. Newly cleared agricultural plots are often established in secondary forest (*purma*), resulting in a relatively short (a few decades or less) rotation system, but they are also sometimes cut from much older forest, as in the example shown here. The construction of the Iquitos-Nauta highway opened a large area of formerly inaccessible forest to settlement, resulting in a first wave of rapid clearing along the highway corridor. In this example, about one kilometer from the road, the interface between mature forest and a new plot of rice and yuca is extremely abrupt. Note also the hilliness of the site, characteristic of many of the region's terra firme landscapes.

Photo 1.17. A ‘hard’ forest edge such as this one, where mature forest immediately abuts a newly cleared area, alters microclimate conditions inside the remaining forest. In particular, increased light and ambient temperatures, and altered airflow patterns, can increase forest plant desiccation near the edge. Some bird species avoid such edge conditions, while others are attracted to them.

Photo 1.18. The immediate surroundings of small *ribereño* communities along rivers in Loreto are maintained in permanently open, grassy conditions with various useful trees and shrubs, transitioning quickly to secondary forest (*purma*), small agricultural fields (*chacras*), and várzea vegetation.

Photo 1.19. Very large expanses of deforested land exist near Iquitos, the region's population center, whereas deforestation in the wider region normally comprises small, isolated areas near rivers. As a result, mature forests near Iquitos are often significantly more fragmented, or occur within closer proximity to cleared landscapes. This photo shows overgrown agricultural plots. Note also the clay soils, typical of the region.

Photo 1.20. These leaves of Irapay (*Lepidocaryum tenue*), a small understory palm, were harvested from a mature forest near the Yaguasyacu River in Loreto. Irapay is used as a roofing thatch throughout Loreto, and is an important economic resource for many rural communities. The plant typically grows in dense stands, called *irapayales*, on relatively nutrient-poor soils. *Irapayales*, which can be quite extensive where conditions are good, constitute a distinctive avian understory habitat, and can be significantly altered by heavy exploitation. Extractive activities such as this occur widely around rural communities, and may be spatially associated with forest fragmentation.

Photo 1.21. This partially-finished canoe was being carved at the site where the parent tree was felled, in mature, terra firme forest near the Tahuayo River in Loreto. It had not been worked for some time, when the photo was taken, and may have been an abandoned project. Small scale extractive activities such as this are common near *ribereño* communities, and collectively constitute a complex set of anthropogenic influences on forest habitat characteristics.

Photo 1.22. This Spix's Guan (*Penelope jacquacu*) was shot by a hunter near the Tamshiyacu River in Loreto. Guans and other members of the avian family Cracidae are used for food. This species remains fairly common despite hunting pressure, while the larger-bodied Curassows have become quite rare near populated areas.

Photo 1.23. This hunter was walking back to his house near the Tamshiyacu River in Loreto, after a morning in the forest. He had killed a Spix's Guan (*Penelope jacquacu*), also shown in photo 2.2, and collected liana fibers that are used as lashings in building construction. Hunting is often the primary forest activity of men who also opportunistically collect plant materials for various purposes.

Photo 1.24. Feathers and other evidence of hunting are not infrequently encountered along forest trails near *ribereño* communities in central Loreto. Those shown here were removed from a Tinamou (*Tinamus spp*.); the shotgun cartridge used to kill the bird can be seen at the bottom of the feather pile. Several such feather piles were found along approximately two km of hunting trails over 10 days of using the trails for access to a bird survey site, and White Throated Tinamou (*Tinamus guttatus*) was common in the area.

Photo 1.25. This Red-throated Caracara (*Ibycter Americanus*), a species known for its unpleasant tasting meat, was shot by a local man near the Nanay River, not far upriver from the city of Iquitos.

typical hunting activities in the Peruvian Amazon. Game bird hunting is often a subsistence activity, but some meat is also brought to regional markets. The eggs of large, ground-nesting species, particularly Tinamous, are also collected for food (Photo 1.26). Birds commonly collected for the pet trade are mainly parrots (Psittacidae—Photo 1.27). The primary effect of these activities is to reduce abundances of hunted and collected species, but a related indirect effect may be density compensation—an increase in abundances of species which are ecologically similar to, and in competition with, hunted species, but that are not themselves preferred by hunters (Bodmer and Puertas 2000, Peres 2000a).

The strength of human influence on bird populations can depend on a site's accessibility and proximity to human habitations and agricultural areas at the local scale, and on an area's proximity to urban markets at the regional scale (Sierra 1998, Peres and Lake 2003). However, hunting intensity and the intensity of other extractive activities that may indirectly influence bird populations can also depend on the configuration of areas with different land covers and under different management regimes (Parry et al. 2009). Hunters may kill animals only opportunistically in second-growth forest patches near their homes, for example, as they traverse such patches on their way to preferred hunting areas within mature forest. Local agreements between communities may also partly restrict which forests hunters use. Thus, simple distance or travel time may represent coarse surrogates for hunting intensity that could be improved with more detailed landscape information.

Photo 1.26. These eggs of a large Tinamou (*Tinamus sp*.) had been harvested from a nest that was found near a hunting trail in mature forest, and were eaten by this man's family in their home inside the Tamshiyacu-Tahuayo Communal Reserve in eastern Loreto. Bird eggs, if found, are likely to be opportunistically harvested as an occasional protein supplement.

Photo 1.27. This Scarlet Macaw (*Ara Macao*) had been shot in the wing while flying over an open field near the Yaguasyacu River, and the new owner planned to sell it in Iquitos. The impact of such small-scale, opportunistic hunting for the bird trade is much less important than professional (though illegal) trapping operations.

RESEARCH AGENDA

Comparative framework

Evolutionary diversifications are in part the result of past ecological processes, and current ecological processes are continuing to influence the evolution of biological diversity. Dispersal limitation is also linked closely to ecology and history, because the dispersal of many species depends on interactions with other species as well as landscape features that facilitate or inhibit movement, and dispersal mechanisms are evolved over long historical periods. Evolutionary processes are typically studied across broader spatial and temporal scales than are ecological processes, but ultimately an understanding of biogeographic diversity will demand that all processes contributing to that diversity be viewed integratively (Blondel and Vigne 1993, Ricklefs and Schluter 1993).

Tuomisto and Ruokolainen (1997) and Tuomisto (2007) have suggested that historical explanations should only be invoked when current ecological conditions cannot sufficiently explain observed patterns. The idea that coarse-scale biogeographic regions are a residual product of long-term vicariance and dispersal histories may be supported if the explanatory power of regional boundaries remains evident after present-day environmental variation and geographic distances among sites are taken into account. Similarly, If distances among sites explain differences in species assemblages better than environmental variables such as plant community differences, then species dispersal limitation may influence community structure independently of environmental context (Hubbell 2001, Condit et al. 2002). Proxies for historical, environmental, behavioral, and other factors can, ideally, be measured relative to one another so that when they are not

mutually exclusive, their collective contributions may be considered, and when they are, competing hypotheses may be examined. Thus, the comparison of taxonomic (species, genus, etc.) assemblages across multiple sites where those proxies have been measured is a powerful tool for biogeographic explanation, though one that has seldom been employed for understanding Amazonian wildlife distributions and diversity.

It should be noted that comparisons of individual species ranges, or of species assemblages at multiple sites, cannot constitute a test of hypotheses regarding the role of historical factors in the evolution of species diversity in the Amazon basin, since different hypotheses often produce similar predictions for current species distribution patterns (Moritz et al. 2000, Aleixo 2004). However, it is important to know the degree to which evolutionary-historical factors in general have contributed to current biogeographic patterns, independent of environmental conditions, dispersal limitation, and anthropogenic factors measured on recent, ecological time-scales. Some components of species composition that are inexplicable in terms of these recent influences may correlate well with the coarse-scale biogeographic patterns created by evolutionary diversifications.

Spatial scale

Relationships between bird communities and other landscape features that are evident at one scale may or may not occur at other scales (i.e., relationships may or may not be *scalable*), and this effect is of consequence for understanding distributional patterns and processes (Wiens 1989, Wiens et al. 1993, Forman 1995, Schneider 2001). For example,

historical climatic variability may affect species distributions across spatial extents that include whole regions, but is less likely to be important within much more local spatial extents (for the purposes of this discussion I use the word scale to indicate spatial extent, rather than resolution). In contrast, current ecological conditions may be important at any scale, but may have different effects at different scales, depending on the ecological requirements of particular species and the distributions of their habitats (Lomolino and Heany 2004). In the Amazon basin, for instance, variation in soil characteristics can be quite strong locally, as in the case of small patches of white sand near Iquitos, Peru. Soils also vary at intermediate spatial scales, according in part to regionally important geomorphologic features such as the Nauta formation in northeastern Peru. At the continental scale, soils differ strongly between the eastern and western portions of the basin, according to continental-scale geomorphologic processes associated with the Andean orogeny.

Species assemblages are ultimately a product of processes occurring at all spatial scales. However, most biogeographic studies of Amazonian biota have occurred at continental spatial scales, because their focus on the evolution of taxonomic diversity has been approached chiefly through the examination of species distributional limits. Most described Amazonian bird species have distributions covering considerable fractions of the entire basin (Ridgely et al. 2005, Ridgely and Tudor 2009), so that any division of the basin into distinctive areas based on distributional limits will result in relatively few (seven to ten), large areas (e.g., Haffer 1969, Fjeldsa 1994, Bates et al. 1998, Racheli and Racheli 2003, Nores 2004). The recognition of these distinctive sub-continental areas

may be critical for understanding evolutionary processes and overall species diversity. They may also be important for understanding local communities to the extent that large-scale distributional patterns determine the regional pool of species that can potentially colonize a local area.

Incomplete knowledge of species distributions, though, should indicate caution in drawing conclusions on the basis of those distributions. Bird populations have been located far outside their respective species' known ranges when the appropriate habitat has been surveyed (Aleixo et al. 2000, Alvarez and Whitney 2003). Moreover, species distributions are patchy within overall ranges, limiting the utility of large-scale distributional information in the absence of more detailed information about local ecological processes (Beehler et al. 1995, Aleixo et al. 2000, Thiollay 2002a). There is a gap here in Amazonian wildlife studies, because most ecological investigations have occurred at the opposite extreme of spatial extent, in which the influence of local habitat conditions on species abundances is considered. Only one or two large plots near biological stations are typically employed in such investigations.

Investigations of biogeographic patterns and processes, including human activities that affect plant and animal communities or populations, have increasingly been undertaken at landscape and regional scales by geographers and conservation planners alike (Young 1998, Zimmerer and Young 1998, Ferrier 2002, Rouget et al. 2003, Pressey 2004). These scales lie somewhere between continental and local spatial extents, on the order of tens or hundreds of square kilometers. Focus on these scales derives partly from an interest in biological processes at these scales per se, but also from the social and

political realities that partly determine conservation activities and the scales of human settlement patterns and resource use (Zimmerer and Young 1998). These intermediate scales are also the scales at which within-country biogeographic regions have been outlined for avian taxa (Wege and Long 1995, Rodríguez and Young 2000, Thiollay 2002a). Thiollay (2002b, a) surveyed forest sites distributed within French Guiana and found important avian species composition differences among three major zones from north to south. In Peru, a group of biologists familiar with the country's biota was assembled to outline distinctive regions on the order of hundreds of square kilometers for birds, plants, and other groups (Rodríguez and Young 2000). The regions they hypothesized for different groups were not congruent with one another, and this possibility needs to be tested empirically. Large knowledge gaps exist at landscape and regional scales for even general distribution patterns for many taxa in many tropical regions, so that these intermediate scales constitute an important spatial frame of investigation not only for applied conservation and development agendas, but also for basic biogeographic research (Rodríguez and Young 2000).

Additional considerations

Research agendas in Amazonian biogeography should be informed by physical-geographic, evolutionary, genetic, and ecological inquiry as well as by applied work in conservation, resource management, and development planning. While biogeographers will be most interested in understanding patterns and processes mechanistically, the only

real requirement for applied research is the predictability of those patterns and processes from limited datasets. The latter goal is the subject of much of the following chapter.

Trajectories of research on the evolutionary biogeography of Amazonian birds, as outlined above, immediately suggest several paths for further investigation. For understanding evolutionary history, much progress stands to be made in coupling genetic research with work in physical geography. Evolutionary ecological research that sheds light on the question of whether or not speciation has frequently occurred without allopatric separation of populations will also deeply influence interpretations of how historical physical-geographic events and habitat selection have influenced species diversity and distributions (Fine et al. 2005, Patten 2008). While evolutionary processes are not the focus of this dissertation research, they are a closely related topic of interest for future work.

Field sampling has been, and will remain, the backbone of biogeographic description (Whittaker et al. 2005). However, methodological advances in field sampling have been outstripped by interest in developing methods for maximizing the information that can be extracted from existing field data, museum specimens, and from remotely collected data. Such methods include species and community distribution modeling, establishing surrogacy relationships among taxa and between taxa and environmental variables, the application of remote sensing technologies to distribution modeling, and phylogeography studies using improved genetic sampling of museum specimens. Important advances stand to be made by using the data needs of these approaches to explicitly inform field sampling methods. Most recently published phylogeographies, for

example, have utilized only pre-existing collections, which are typically sparse and geographically ad-hoc, relative to the needs of phylogeographic study design. Field seasons should be carefully designed to fill in geographic, environmental, and phylogenetic gaps in existing collections, and thereby complement and improve existing collections. This will require careful cataloguing of existing museum data, attention to the environmental and biogeographic information available in satellite imagery and botanical survey data, and willingness to work in places that are difficult to access. Some of these field sampling considerations are detailed in the following chapter.

Chapter Two

Biogeographic Research for Wildlife Conservation in the Western Amazon

Geographers have long pointed out a role for biodiversity conservation in the maintenance of healthy societies. Conservation and development initiatives have become increasingly integrated in Latin America as in other regions, and biogeographic information in turn plays an important role in the implementation of conservation agendas (Margules and Pressey 2000, Zimmerer and Carter 2002, Mäki 2003, Whittaker et al. 2005). The ways in which biogeographic information is produced can influence conservation outcomes, including what elements of biodiversity are perceived to be important, where conservation efforts are focused, what activities take place there, and what constitutes conservation success. This has been true in the Amazon basin, where changing understandings of the region's biogeography have resulted in changing foci of conservation agendas (Schulman et al. 2007). In Peru, the variety of conservation lands that exists today reflects a legacy of both historical continuities and variations in not only the degree to which natural history and biodiversity assessments have been consulted, but also the kinds of assessments that have occurred (Young and Rodríguez 2006). Given this situation, forms of biogeographic representation have increasingly been developed with

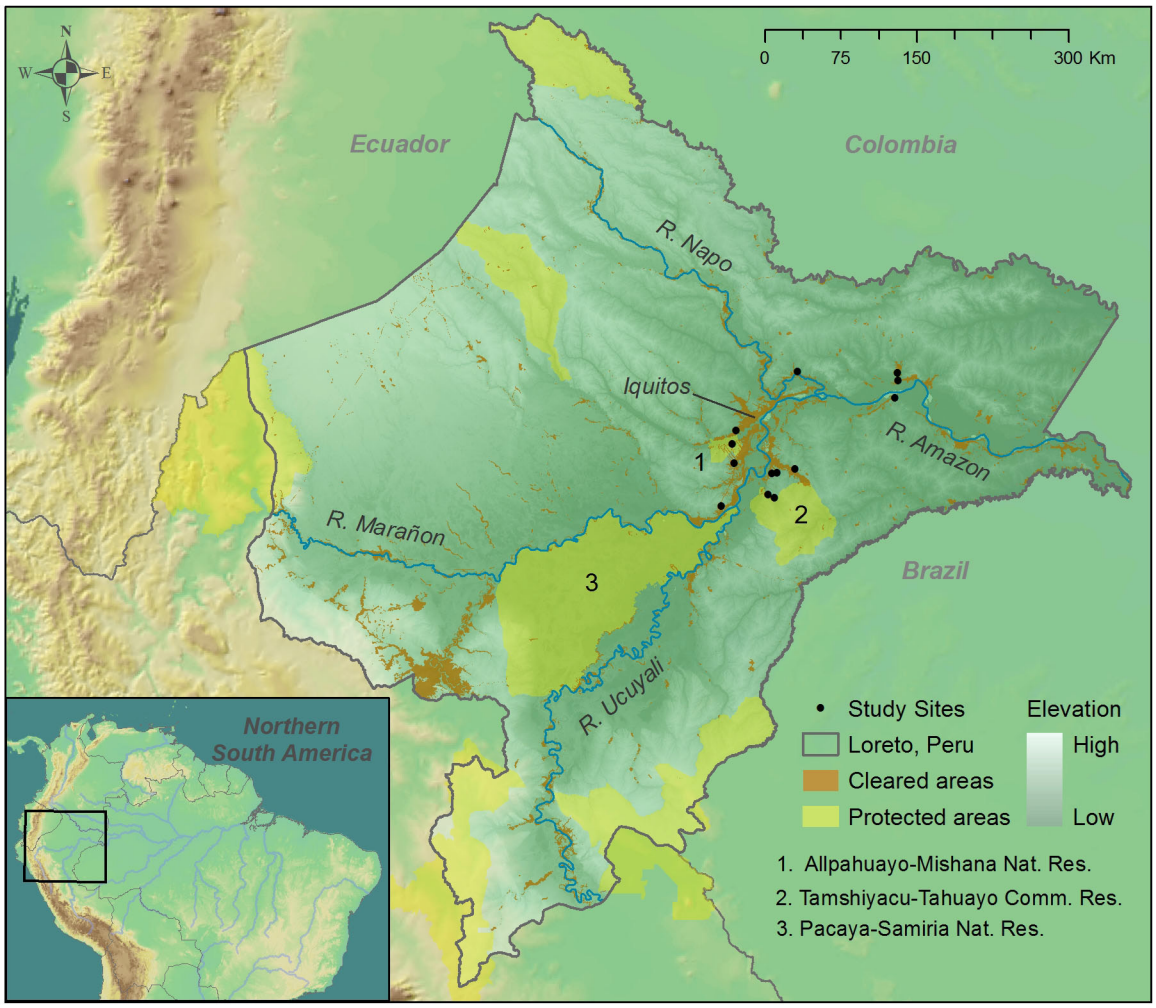
the specific goal of maximizing their applied utility, in terms of conservation outcomes. This relationship should be beneficial for biogeography inasmuch as it drives the development of methods that maximize the amount of new biogeographical understanding that can be derived from necessarily limited field efforts and datasets. One risk, on the other hand, is that thorough and carefully measured assessment is compromised in the rush to produce useful results, with poor conservation outcomes following poor science. The most desirable outcomes probably result from approaches that are designed with their eventual applied uses in mind, recognizing that future conservation successes depend, as they have in the past, partly upon the rigor of biogeographic approaches.

My research is driven in part by a perceived need to develop biogeographic knowledge that is of relevance to conservation problems. As various forms of development occur in the Amazon basin, depictions of regional biodiversity will be important tools for making decisions about the location and management of conservation and development activities (Margules and Pressey 2000, Rodríguez and Young 2000, Ferrier 2002, Mäki 2003). This project's study area, a region centered around Iquitos, Peru, is of particular interest because the development of urban, agricultural, and forestry landscapes is occurring at a rapid pace. Iquitos is the largest city in the western Amazon, and the need for geographic information to inform development planning in the region has been stressed by Peruvian governmental organizations as well as non-governmental organizations (BIODAMAZ 2001, Mäki 2003, Schulman et al. 2007, Finer et al. 2008, Salo and Toivonen 2009, SERNANP 2009) .

CONSERVATION IN LORETO

Iquitos is situated on the main stem of the Amazon River, and is the capital of Loreto, Peru's largest department (province). The vast majority of Loreto is low-elevation Amazonian forest, but it also extends westward into the eastern Andean foothills (Map 2.1). Conservation activity in Loreto, as in Peru as a whole, has been characterized by the formation of protected natural areas at the level of national government, but modified approaches have also appeared more recently, importantly including communal reserves designed around principles of sustainable resource use. This trajectory broadly resembles the situation in developing countries more generally, where emphasis has historically been placed on preservationist principles at the level of national government, but the sustainable development movement and neoliberal policies have shifted focus towards sustainable resource use and more local scales of governance (Sheth 1997, Adams 2001, Schaik and Rijksen 2002, Zimmerer and Carter 2002). Nonetheless, the conservation of biodiversity per se has remained a consistent priority underlying the development of Peru's system of conservation areas up to the present (Young and Rodríguez 2006, SERNANP 2009).

The most visible conservation activity in Loreto has been the formation of large protected areas, of which the most well known are Pacaya-Samiria National Reserve, the largest such reserve in Peru, and Cordillera Azúl National Park. These remain the only large protected areas with significant enforcement in Loreto, although several other



Map 2.1. Loreto is the largest department in Peru, and lies almost entirely within the western Amazon basin. Deforestation is limited, and chiefly concentrated around the few large cities and towns, which themselves are located along major rivers. This project's study sites were located inside and outside protected areas near the city of Iquitos, both near and far from areas extensively cleared for agriculture.

Reserved Zones exist and may be under consideration for the formation of new parks or reserves (SERNANP 2009). Allpahuayo-Mishana National Reserve, a small reserve near the outskirts of Iquitos, was formed in large part to protect rare, nutrient-poor 'white sand' forests, which are known to harbor an unusually high number of endemic species. Several bird species of conservation concern occur in the reserve, and these were highlighted in arguments supporting establishment of the reserve (Alvarez and Whitney 2003, Whitney and Alvarez 2005). The biological uniqueness of the white sands forests provided the initial reason for establishing a reserve, but additional rationales that eventually proved critical to the successful legal designation of the reserve included subsistence and sustainable development opportunities for local communities, as well as environmental services (namely the drinking water supply for Iquitos) at the regional level (Salo and Pyhala 2007). One of this project's study sites was located within the Allpahuayo-Mishana National Reserve, and two were located immediately outside the reserve's border.

The Tamshiyacu-Tahuayo Communal Reserve, located about 100 km south of Iquitos, contains zones designated for subsistence use as well as fully reserved zones. Efforts to create the reserve began after local ribereño communities placed significant pressure on the Peruvian government to control what they perceived to be excessive resource extraction by nonresidents (McNeely 1995, Bodmer and Puertas 2000). Today it exists as the first officially designated communal reserve in a series of planned protected areas at the Regional Government level within Loreto. Another priority area under consideration by the regional government project is a large area containing portions of

the watersheds of the Ampiyacu, Apayacu, and Algodón Rivers, east of the Napo River. The strong presence of indigenous and non-indigenous rural communities with traditional land use practices has thus given conservation efforts in Peru, as in other developing countries, a distinctive signature inasmuch as efforts to prevent environmental degradation have been explicitly tied to the preservation of rural livelihoods and cultural traditions (Guha 1989, McNeely 1995, Sheth 1997, Tokar 1997). Two of this project's study sites were located in the Tamshiyacu-Tahuayo communal reserve, and two sites were located in the Ampiyacu watershed (Map 2.1).

Conservation lands represent a small fraction of Loreto's total land area. Outside those areas, resource extraction is controlled to varying degrees on a significant amount of land under other legal designations, including titled indigenous territories. Nearly one third of the department's area has been designated as timber concessions and production forests, where resource extraction is in theory controlled by national natural resource agencies; these areas overlap with reserved zones in some cases (Salo and Toivonen 2009). Oil and gas exploration concessions exist across three-quarters of Loreto's area, overlapping widely with forestry areas, indigenous territories, reserved zones, and communal reserves—the only areas excluded from oil and gas concessions are national parks and reserves (Finer et al. 2008, Salo and Toivonen 2009).

REPRESENTATIONS OF BIOGEOGRAPHIC INFORMATION

Regardless of the simplicity or sophistication of maps and other tangible representations of biogeographic information, all such representations are models of one kind or another, built to some degree from taxon location data and information (or assumptions) about relationships between organisms and their environments. Species range maps, niche models, areas of endemism, ecoregions, and other representations all make inferences from limited empirical data in order to come to more general understandings of biogeographic phenomena. The recognition that field sampling will normally be extremely limited in comparison to the level of detail that biogeographers and conservation planners would like to have about biogeographic distributions has led to important innovations in distributional modeling, some of which are described here.

In a sense, maps and other distributional models are end products of biodiversity location assessments, because they compile information and present it in a useable format. However, they also serve an important active role in assessment, and should not be seen merely as end products. This is because such maps are never complete and are never without uncertainty, and they therefore suggest, in specific ways, new activities for biodiversity assessment. For example, ecoregion maps are based primarily on the distribution of vegetation types (Dinerstein et al. 1995, Grossman et al. 1998), but it is uncertain how well those vegetation types represent the distributions of animal populations (e.g., MacNally et al. 2002). This immediately suggests that the investigation of animal habitat selection and occupancy, at regional scales, will improve ecoregion maps, and perhaps complexify ecoregional concepts. Furthermore, models are valued as

predictive tools, and they focus field efforts by helping us predict the most productive places to collect data. Thus, maps, as is true of any kind of model, exist in a mutually informative relationship with empirical data. The forms of biogeographic modeling described in this section should be viewed in that light.

Species distributions

Attempts to understand the geographic distributions of individual taxa, usually species, have been central to biogeographic and evolutionary studies (Darwin 1859, Simpson 1965, Gaston 2003). They are also critical for conservation planning, because the location of conservation activities and protected areas should be based partly on knowledge about which species occur where (Margules and Pressey 2000). Historically, representations of species distributions have been based largely on field-collected museum specimens and expert knowledge, resulting in traditional outline-style range maps that often neglect internal variations in abundance (Sánchez-Cordero et al. 2004). More recently, Geographic Information Systems technology has allowed spatially explicit modeling of species distributions with location data and environmental data. Species location data are associated with environmental variables (e.g., elevation, rainfall, temperature, soil type) through statistical models such as logistic regression and Bayesian maximum entropy, or genetic algorithms such as that used in the Genetic Algorithm for Rule Set Prediction program (Stockwell and Peters 1999, Anderson et al. 2003, Sánchez-Cordero et al. 2004). Models can then be projected onto continuous geographical space, extrapolating and

interpolating probability of occurrence estimates from the original specimen locations to all areas where the species is expected to occur.

The process described above may be best conceptualized as niche modeling, because models will return the locations of all areas that, according to the environmental parameters used in the model-building process, are similar to those areas where the species has actually been detected in the field (Anderson et al. 2003). That area may be thought of as the species' fundamental niche, whereas the species may only actually occur within a more restricted area, its realized niche (Hutchinson 1957, Pearman et al. 2008). Basic outline maps representing peripheral range limits therefore usually remain useful in conjunction with niche modeling exercises, because niche models may 'overpredict' the geographic extent of the realized niche. On the other hand, in cases where distributions are very poorly known, spatially explicit distribution modeling may provide a means of predicting and discovering occupied areas outside known range limits (Sánchez-Cordero et al. 2004), as well as identifying suitable areas that are currently unoccupied.

Advances in spatially explicit distribution modeling are promising both for basic distribution mapping and for understanding species-habitat relationships, but data deficiencies and model uncertainties still necessitate extreme caution in the use of sophisticated modeling approaches for making conservation decisions. Especially when models are built for many species in order to evaluate community compositions at multiple locations, many small errors have the potential to add up to large mistakes (Loiselle et al. 2003). Even for individual species, if fundamental or realized niches are

not static across space or time, niche models which rely on a single modeled relationship between environmental parameters and species occurrence may not depict occurrence accurately across the area or timeframe included in the model (Pearman et al. 2008). Niche models developed from species occurrence and environmental data in one region can almost entirely fail to describe the species' distribution in another region (Pearman et al. 2008, Stralberg et al. 2009).

Community distributions

Representations of biological community distributions include such concepts as biomes and ecoregions at large spatial scales, or habitat types at smaller spatial scales (Brown and Lomolino 1998). Ecoregion maps are widely used by conservation organizations, because they provide a clear biogeographic framework within which to prioritize areas for conservation (Dinerstein et al. 1995, Jepson and Whittaker 2002, Taulman and Smith 2002, Wikramanayake et al. 2002).

While maps usually convey community distributional information by depicting cleanly segregated ecoregion or habitat types, it is widely recognized that gradual transitions between community types are more common than clean, abrupt divisions. Moreover, there are fundamental difficulties with typological representations of ecosystems at nearly any spatial scale, because communities are composed of species whose distributions are not always tightly correlated with one another. As species individualistically respond to changing (in space or in time) environments, communities vary in such a way that any particular place or time is unique (Gleason 1939, Whittaker

1978, Austin et al. 1984). Nonetheless, broadly similar environmental conditions between areas within reasonable spatial proximity of one another frequently lead to broadly similar biological community compositions, so that typological representation can have practical utility (Whittaker 1978, Pressey 2004). In the Amazon basin, there is a dearth of research investigating spatial associations between wildlife distributions and other landscape characteristics, and it is therefore still an open question whether or not typological distinctions can accurately or adequately represent Amazonian wildlife diversity.

The application to community distributions of modeling approaches that are conceptually similar to species distribution modeling have been suggested, although the multitude of dissimilar, partially overlapping species distributions that determine community compositions suggest an extremely complex modeling process (Ferrier 2002). However, if most species do respond to environmental gradients, and the set of basic environmental variables that most species in a region respond to is manageably small (even if different species respond in different ways to the same variables), then mapping spatial variability in community composition on the basis of environmental data may be tractable (Pressey 2004). It is important to note that while this approach would allow prediction of distinctiveness among areas, it would not necessarily allow the prediction of which particular species occur in each area; that task would still be left to individual species distribution models.

Surrogates for Biodiversity

In theory, the conservation of biodiversity involves an interest in, and knowledge about, all forms of biological diversity that may exist in a region. Biodiversity may include genetic diversity at any taxonomic level, behavioral diversity such as differences in migratory behavior within genetically similar groups, and other forms of phenotypic and ecological diversity (Sarkar and Margules 2002, Maclaurin and Sterelny 2008). In practice, we are only able to measure a very small portion of total biodiversity, and must make decisions about all biodiversity on the basis of the quite limited information that we have. Surrogates are biological taxa or environmental variables whose distributions correlate closely with those of taxa that are of interest, but are more difficult to assess (Landres et al. 1988, Caro and O'Doherty 1999, Caro 2002, Ferrier 2002, Sarkar and Margules 2002). Changes across space or over time in target systems can be inferred from changes in surrogates. The predictive relationship between surrogate and target is therefore critical. The problem of ensuring that the relationship is in fact reliable has been termed the 'surrogacy problem' in conservation biology (Sarkar and Margules 2002). The primary goal of surrogacy is to make the use of limited field data as efficient as possible for representing the distributions of biodiversity, so the subject of surrogacy is intricately tied to field sampling methods and to modes of representing biogeographic information.

Conservation planning decisions can in theory be made relevant to the distributions of far more elements of biodiversity than are actually measured, if field work can indeed identify and be focused onto good surrogates. Surrogacy concepts such as focal species, umbrella species, flagship species, and indicator species have been

developed for this purpose, but measures of their actual utility have had mixed results (Simberloff 1998, Caro and O'Doherty 1999, Andelman and Fagan 2000, Caro 2003). Biodiversity indicators or surrogates, as defined here, differ from umbrella, flagship, and focal species, because those are typically chosen for their heightened sensitivity to anthropogenic landscape changes. For example, a useful umbrella species responds differently than most species to increased forest habitat fragmentation because it suffers more rapid decline, and it will be the last species to recolonize a restored habitat. In contrast, a biodiversity surrogate will vary in concert with the target species or community, so that changes in one can be inferred directly from changes in the other (Caro and O'Doherty 1999).

The concept of surrogacy has developed primarily in the field of conservation biology as a means of prioritizing sites for conservation or restoration. Tests of surrogacy (especially umbrellas, focal species, and indicators) have been conducted by assessing the degree to which surrogate distributions are congruent with the distributions of target biodiversity, but it has recently been recognized that this criterion is unnecessarily restrictive (Andelman and Fagan 2000, Garson et al. 2002). All that actually needs to be known is the degree to which area prioritizations based on surrogate distributions, and resulting conservation reserve networks or restoration sites, end up representing the desired target biodiversity. Because areas selected for conservation prioritization are nearly always much smaller than the entire distributions of either surrogates or targets, this less ambitious goal may be satisfied even when congruence among surrogate and target distributions is not exceedingly high. For a surrogate to be useful, site selection

using that surrogate should do a better job than random site selection at representing target biodiversity. Maximal utility of surrogates is achieved by identifying the particular surrogate or set of surrogates, from all of those available, that does the best job (Garson et al. 2002, Higgins and Ruokolainen 2004). In this sense, the environmental variables which prove to be most useful in modeling biological community distributions (discussed above) may also prove to be extremely useful surrogates, particularly because they may be much easier to measure in the field than are the abundances of large numbers of species (Ferrier 2002, Pressey 2004, Sarkar et al. 2005).

Clearly, not every project can rigorously test the assumptions that are made when surrogates are used. Otherwise, the work-saving purpose of surrogates would be negated (Simberloff 1998). However, priority should be given to establishing relationships between surrogates and targets before they are widely used, and projects that use surrogates without testing them should select surrogates that have been tested previously. The reliability of indicators has been empirically tested in this manner relatively few times, and results have been different for different researchers and different ecosystems. Studies demonstrating failure of surrogates or indicators suggest that the concepts should be used cautiously (Andelman and Fagan 2000).

Birds have perhaps been the most commonly invoked indicator species, probably because they are charismatic and relatively easy to survey, yet very few true tests of their ability in this regard have been conducted (Lindenmayer and Fischer 2003). In one rare example, Rubinoff (2001) tested the ability of the California Gnatcatcher (*Polioptila californica*) to represent the distributions of three Lepidoptera species in coastal scrub

habitat, and found no correlation among distributions. Even the less stringent requirements imposed on an umbrella species (not necessarily similar distributions, but at least nested distributions) were not met, because the butterflies were found to occur only in the largest patches of coastal scrub, whereas the bird occurred in much smaller patches. The California Gnatcatcher has been used as an umbrella species for coastal scrub habitat management, but may not be suited for that role (Rubinoff 2001).

At the global scale, it is not certain that focusing on bird conservation will result in effective conservation of other wildlife groups. Naidoo and Adamowicz (2000) studied the effect of economic prosperity on the number of threatened and endangered species at the national level. The theory that economic prosperity leads eventually to increased conservation interest and effective management of threatened species was supported only for birds, but refuted for plants, reptiles, amphibians, and invertebrates. It is thus possible that interest in birds as surrogates for ecosystems will end up leaving other taxa behind.

Some tests of surrogacy have produced positive results, suggesting that, while the concept must be used with caution, it may prove effective when relationships between surrogate and target are established empirically. Garson et al. (2002) found that site prioritization on the basis of bird distributions was able to capture a targeted number of occurrences of threatened and endangered species better than was a prioritization on the basis of random site selection. Again, though, these results do not confirm the superiority of birds over other potential surrogates, because other surrogates were not tested.

Steps have been taken by some researchers to develop a systematic framework for selecting indicators, primarily in the field of conservation planning. Two basic

approaches to systematizing the process of selecting indicators have been taken. One of these focuses on systematizing the efforts of experts to apply their knowledge of ecosystems and focal species concepts to select surrogates (Beazley and Cardinal 2004). This approach incorporates general knowledge about the distributions and life histories of organisms, but does not empirically test the validity of its conclusions. The second approach searches for surrogates in existing datasets by empirically testing the ability of particular species or groups to represent patterns in the whole dataset (Higgins and Ruokolainen 2004, MacNally and Fleishman 2004, Manley et al. 2004). This approach may lack generality, but it is the only approach capable of verifying the effectiveness of surrogates. The task is formidable, though, because it requires collecting a dataset that represents the entire community that has been targeted for representation with indicators. Once this dataset exists, conclusions from trial indicator datasets (subsets of the larger dataset) can be compared directly to conclusions based on the larger dataset. Manley et al. (2004) suggest that in situations where a sufficient dataset may not initially exist to systematically select good surrogates, the process of surrogate selection can be incorporated into monitoring within an adaptive management framework. As the project proceeds and datasets are accumulated, they can be explored for the selection of increasingly useful surrogates.

MacNally and Fleishman (2004) were able to identify a group of five Lepidoptera species that served as very good indicators of total Lepidoptera species richness across large areas of a mountain range in western North America, and successfully validated the selection of indicators in another mountain range within the same region. The ability of

both MacNally and Fleishman (2004) and Higgins and Ruokolainen (2004) to identify strong indicators of change in community composition among target taxa probably resulted from their unique approach to the selection of indicators. In each case, indicators were systematically selected from a very large number of possible indicators by testing the effectiveness of each possible indicator, where indicators may have been individual species or groups of species defined taxonomically, ecologically, or physiognomically. In most tests of surrogacy, by contrast, only a small number of possibilities are explored, and these are often based on preconceived notions of umbrella or focal species status.

The use of biological or environmental surrogacy concepts is common in various applications of ecological assessment, monitoring, and planning. This is natural, because survey data are always limited, and one always wishes to maximize the information available in one's data. However, there is a temptation to use surrogates and indicators uncritically, and empirical tests of their utility are often seen as either unnecessary or requiring extra work that could be allocated to other priorities. The potential utility of these tools demands that additional empirical tests be conducted in many different ecosystems to determine the best methods for selecting surrogates or indicators. When the spatial, taxonomic, and ecological parameters used to define surrogate species, groups, or environmental features have been set to maximize the efficiency of surrogates, and when the conditions are appropriate and the limitations are known, conclusions drawn from surrogacy relationships may be well-defined and reliable. A particularly promising avenue of research is the systematic search for maximally effective surrogates,

and environmental surrogates may eventually be found by this approach to be broadly useful.

FIELD SAMPLING METHODS

Historically, most field sampling of species locations has been ad-hoc, in the sense that spatial sampling schemes have not been explicitly designed with coverage of undersampled habitats, undersampled areas, or undersampled taxa in mind (Austin and Heyligers 1989, Margules et al. 2002). The primary challenge for improving field sampling methods will be to incorporate principles of systematic sampling that are designed to maximize the utility of limited field data for modeling biogeographic distributions in areas where field work has not been done, for biota that have not been sampled, and for time periods that have not been sampled. Any compilation or representation of field-collected location data involves some kind of modeling, and field data collection should therefore be viewed as part of the model-building process, rather than as an alternative to model-building.

Environmental data and environmental gradient sampling

One of the most pronounced shortcomings of current field sampling methods is that environmental variables, which may render critical information about the habitat associations of biota, are not sufficiently measured. Museum specimens and observation records may have basic location data, with minimal or no quantitative descriptions of the

locations attached. If the location data are reliable, environmental data may be retrieved by returning to the site, but there is no guarantee that conditions at the site will not have changed significantly since the specimen was collected or observed.

A more serious issue concerning environmental data may be that distinctive environments have not been sufficiently sampled, and that issues such as site accessibility, political instability in some countries, and general poor planning may have introduced bias in which environments are typically sampled (Austin and Heyligers 1989, Margules et al. 2002). Even geographically uniform or randomized sampling may not sufficiently capture environments that are particularly rare but remain interesting, perhaps because they contain endemic species. Biological field sampling is maximally useful for understanding species-habitat relationships as well as for conservation planning when known distributions of environmental factors representing hypothesized habitat types are used to design representative field sampling schemes (Austin and Heyligers 1989, Haila and Margules 1996). This essentially involves hypothesizing environmental surrogates for biodiversity and testing them by collecting biological data across spatial gradients in environmental surrogate values. The use of Geographic Information Systems can greatly facilitate the design of field sampling schemes with multiple forms of environmental data (Franklin et al. 2001).

Field taxonomy

There still exists a critical role for field sampling in the observation and collection of undescribed biota (Meadows 2001, Whittaker et al. 2005). The large majority of species remain undescribed, and all conservation planning currently assumes that described species are a sufficient surrogate for undescribed species. However, described species are predominantly those large-bodied plants and animals whose presence is the most obvious in the most accessible landscapes. It is unlikely that their biogeography is essentially the same as the biogeography of small, cryptic invertebrates and organisms inhabiting the most inaccessible places on Earth. Systematic sampling across environmental gradients, giving special attention to rare, undersampled habitat types, will probably facilitate the location of undescribed taxa (although they are not particularly hard to find if one is willing to study non-charismatic taxa in developing countries). The basic biogeographic description of currently unknown taxa should be a priority for future field work (Orians and Soule 2001, Whittaker et al. 2005).

Rapid assessment

Given the vastness of areas for which little biogeographic data exist particularly in developing countries, and the rapidity with which natural landscapes are being drastically modified by people in many regions, there is an incentive to develop methods of collecting basic, extensive data very rapidly (e.g., Conservation International's Rapid Assessment Program, Meffe and Carroll 1997, Schulman et al. 2007). However, rapid assessment methods have suffered from some of the shortcomings discussed above:

quantitative environmental data may not be collected, habitats may not be systematically sampled, and absence and abundance data come with high levels of uncertainty. These may be unavoidable trade-offs in some cases, but the intelligent application of biological and environmental surrogacy concepts in the design of rapid assessment protocols may produce a vastly more efficient use of limited field time (Higgins and Ruokolainen 2004).

Many advances in maximizing the information extractable from limited field data have been driven by the perception that conservation issues are urgent, and that decisions must be made within time frames that do not allow significant increases in the availability of field data (e.g., Meadows 2001). This problem is particularly acute in developing countries, where field data are the most sparse. Effective solutions will involve tailoring approaches to data collection (in the field and remotely) and modeling to the specific needs of appropriate conservation planning methods.

REMOTE SENSING

Individual biological organisms are not usually visible in the remotely sensed data typically used to study landscapes at the broad extents necessary for conservation planning, due to the coarse spatial resolution available from systems such as Landsat Thematic Mapper, NOAA-AVHRR, and SPOT satellites (Kerr and Ostrovsky 2003). However, as data storage and computational abilities of computers advance, data from systems capable of higher spatial resolutions such as IKONOS, as well as digital aerial photography, will increasingly be used at wide spatial extents (Turner et al. 2003). Even

so, it is not necessary to identify individual tree canopies or caribou in imagery if the composite environmental and land cover information available from satellite imagery can be correlated to species or community distributions (Tuomisto 1998, Turner et al. 2003). Efforts to do so for both plants and animals have shown success, suggesting that remote sensing will increasingly be used together with field sampling methods to improve our understanding of biogeographic distributions (Hepinstall and Sader 1997, Kerr et al. 2001, Nagendra 2001, Saveraid et al. 2001, Seto et al. 2004).

The applications of data derived from remote sensing for biogeographic descriptions are potentially broad, including large-scale habitat mapping (Tuomisto et al. 1994, Tuomisto et al. 1995, Sierra et al. 2002), individual species distributional modeling, and the kinds of land cover change analyses that are necessary for evaluating the status of, and threats to, biodiversity at species or community levels (see below). The primary risk in using remotely sensed data, as with all surrogate data, is that relationships between the surrogate data and the actual biogeographic distributions of interest may be misinterpreted or contain error that is not sufficiently accounted for. Thus, empirically establishing surrogacy relationships through the integration of remote sensing and field sampling is critical (Tuomisto 1998). Remote sensing research may be seen as highly dependent upon field sampling (i.e., ground truth data), but in an integrated framework, the reciprocal relationship should also be recognized: field sampling may be made vastly more useful by designing sampling schemes to specifically sample across gradients in remotely sensed data (Millington et al. 2001).

Intelligent decision-making in conservation involves placing information about the location, status, and temporal dynamics of biodiversity together in a decision-making framework with multiple other social and political criteria that land managers must contend with (Margules and Pressey 2000, Possingham et al. 2001, Faith et al. 2003, Schulman et al. 2007). Although biodiversity assessments are only part of the picture, they must remain a very central part, and in this respect, the continued development of tools such as intelligently crafted field surveys, surrogacy analyses, species and community distribution modeling, remote sensing of environmental features, and population viability analyses will remain central to conservation planning. Systematic, algorithm-based approaches to prioritizing sites for conservation attention offer fairly sophisticated means of integrating these tools not only with one another, but also with additional social and political criteria (Margules and Pressey 2000, Sarkar et al. 2004). Tailoring biodiversity assessment tools to the needs of systematic conservation planning procedures can improve the utility of assessment tools. However, systematic planning procedures do not yet offer tools for robustly predicting the priority of conservation areas over moderate time periods when social and environmental contingencies may alter the value of different areas (Meir et al. 2004). Systematic planning procedures also focus conservation efforts on discreet areas, leaving low-priority places to be given conservation attention at some unspecified future time. Furthermore, such prioritizations derive from the identification of conservation targets which are ultimately subjective, and therefore contestable. These may represent problems that can eventually be solved with

increasingly sophisticated systematic approaches, or systematic planning may best be subsumed under some more inclusive category that admits the value of some fundamentally non-systematic aspects of conservation planning—in particular, the non-predictable and locally idiosyncratic interests of local communities and other stakeholders. In one sense, this is already being achieved when multiple systematic prioritization schemes, based on variations in targets and future contingencies, are offered to stakeholders and policy makers to choose from. Either way, approaches that consider whole landscapes integratively will be increasingly important, and methods of tailoring biodiversity assessments to the needs of integrative landscape planning should remain an area of active research.

The long-term conservation goal of this project is to provide information about the distribution of forest wildlife communities that will maximize conservation and development planners' ability to locate conservation activities in areas where they will effectively conserve a representative array of Amazonian biodiversity. If researchers are to take seriously the idea that development should strive to accommodate the maintenance of biodiversity as a cultural good, then biological research aimed at enabling conservation should not be neglected. The goals of biodiversity conservation research, then, are to identify the actual causes of biodiversity loss, and to design activities that effectively distance biodiversity from those threats (Margules and Pressey 2000). In practice, this usually entails the maintenance of indigenous species through maintenance of landscape processes upon which they depend (Sarkar and Margules 2002, Whittaker et al. 2005). Biogeographical research is critical for these goals, because knowledge about

the spatial distribution of biodiversity is necessary for making decisions about the location of conservation activities. This follows from the idea that all biogeographically unique areas should have some form of representation in conservation activities (Margules and Pressey 2000, Rodríguez and Young 2000, Ferrier 2002). While regional plans based on this principle have become pervasive, actual data-driven biogeographic descriptions of tropical regions have not developed proportionately, and such descriptions should therefore be a priority (Sarkar 1999, Sarkar and Margules 2002, Brechin et al. 2003, Wilshusen et al. 2003, Whittaker et al. 2005, Schulman et al. 2007). How are landscapes likely to change in the future as a result of interactions between people and their environments? Geographical representations of biodiversity, together with explanations for why it is there and how it is changing over time, will be essential for answering this question in place-specific contexts.

Unique conservation opportunities exist in developing countries where large, relatively undeveloped areas offer the potential for the creation of new protected areas that might include indigenous reserves, forests managed for extractive activities, and national and provincial parks (Peres 2002). Conservation projects and protected areas might be more intelligently placed to represent patterns of biodiversity than has been done to date throughout much of the world, where economically marginal lands have usually received conservation priority (Margules and Pressey 2000). More broadly, though, such areas offer the opportunity to implement new conservation strategies that learn from past mistakes and successes, focus integratively on whole landscapes and

regional economies rather than just protected areas, and remain maximally sensitive to particularities of place.

Chapter Three

Research Introduction and Study Area:

Bird Communities near Iquitos, Peru

INTRODUCTION AND STUDY AREA DESCRIPTION

My goal was to determine whether variations in bird community composition at landscape and regional scales were associated with geographic and environmental differences among sites. Differences among sites may include their location relative to one another; their location in relation to major dispersal barriers such as rivers; topography and soil characteristics; forest plant age, structure, and species composition; and measures of hunting intensity and agricultural use and history. Each of these factors serves as a means of evaluating more general explanations for biogeographic diversity, which include spatial and temporal variability in historical climatic and geomorphologic processes, present-day ecological conditions, dispersal abilities of different species, and recent human influences (Ricklefs and Schluter 1993, Condit et al. 2002, Nekola and White 2002, Lomolino and Heany 2004). The specific factors that I tested for association with bird community composition, and additional research questions related to those factors, are summarized in Tables 3.1 and 3.2.

Table 3.1. Explanatory variables tested for correlation with bird survey data. Those variables that were correlated with bird community composition became candidate variables for multiple regression models.

Broad-scale biogeography	
Regional:	N or S of Amazon River
Dispersal limits:	Geographic distance, ln geographic distance, Amazon River
Distribution limits:	Species range maps
Local environments	
Topography:	Elevation average, range and variance within 0.15, 0.5, 1, and 2 km of transects
Soil:	Ca, Na, Mg, K and Al concentrations, pH, organic matter, particle size composition
Plant floristics:	Melastomataceae species composition
	Pteridophyte species composition
Forest structure:	Tree size (basal area from DBH); small stems and large stems
	Tree density; small stems and large stems
	Treefall gaps (proportion of transect length in early gap phase)
	Leaf litter depth
Local human influences	
Hunting intensity:	Local community size
	Travel time to local community
	Travel time to regional market
Landscape forest composition within 500 m, 1 km, 2 km, 4 km:	
	Percent open areas/secondary forest
	Percent mature forest
	Length of mature forest edge
	Forest edge-to-area ratio

Table 3.2. Additional research questions concerning relationships among the factors that may influence bird community composition.

Broad-scale (regional) biogeography
Can geographic distance account for spatial variation in community composition that is not associated with regions (opposite sides of the Amazon River)? Can it account for variation that is not associated with known species distributions (range maps)?
Can subspecies distributional limits at least partially explain community composition differences between regions?
Local environments and human influences
Plant community composition is expected to be strongly associated with soil characteristics; can soil characteristics alone account for the component of variation in bird community composition that is associated with plant community composition? Or, is the association of bird community composition with floristics stronger than its association with soils?
Is spatial variation in bird community composition more strongly associated with plant community composition (floristics) or vegetation structure (physiognomy)?
Is community composition more strongly associated with landscape-scale forest structure, in terms of clearing and fragmentation around survey sites, or with more local forest structure at survey sites?
Local versus regional influences
Can local environmental differences between regions explain community composition differences between regions? In other words, can environmental gradients alone explain biogeographic regions?
If there are independent regional and local influences on bird community composition, which are stronger? Do they influence different components of bird communities?

This research draws from several traditional and recent agendas in geography. An emphasis on multiple, potentially interacting explanations for spatial and temporal patterns and processes incorporates interpretations from geomorphology, biogeography, and ecology (Ricklefs and Schluter 1993, Tuomisto and Ruokolainen 1997, Cowell and Parker 2004, Young et al. 2004, Ricklefs 2007). A special interest in landscape and regional scales, on the order of tens to hundreds of square kilometers, reflects a recognition of the particular importance of these scales for development and conservation issues (Young and Zimmerer 1998), but also addresses the need to evaluate interactions between regional and local processes at intermediate scales in order to more fully understand community composition (Holt 1993). An emphasis on basic biogeographic description through field survey also derives from an applied conservation perspective (Zimmerer and Langstroth 1993, Tuomisto and Ruokolainen 1997, Margules et al. 2002, Lomolino and Heany 2004, Schulman et al. 2007). This research is focused on the local bird community, in a particular place and time, viewed as an outcome of the historical and present-day events that have occurred in and around that place. I use a comparative framework to describe how different some bird communities are from others, and to try and explain why they are different. It is hoped that these descriptions will prove useful in attempts to conserve wildlife diversity as the Western Amazon develops.

This research is focused on wild bird communities, so a definition of the wildlife community is in order. I use the word community to indicate the particular composition of a group of birds, where the group is defined by arbitrary spatial and temporal limits, and its composition is described at arbitrary taxonomic levels. Therefore, in the context

of this study, local bird community composition refers to a description of which species or genera are present, in what abundances, at a particular site at the time of a survey. I treat community and assemblage as analogous terms. Both are closely related to the concept of species turnover, which in a geographic context indicates change in the species composition of communities from place to place (Brown and Lomolino 1998). My use of the word community should not be taken to indicate anything beyond this arbitrary descriptive function.

Birds are a logical choice among possible study taxa because they are a well-known group that can be surveyed with relative speed and accuracy, and they constitute a significant component of tropical forests in terms of biomass, diversity, and ecosystem function (Gentry 1990, Gill 2006). Birds were one of the most studied groups in the early days of Amazonian exploration by European biologists such as H.W. Bates (1863) and A.R. Wallace (1876), and have remained so ever since. As a result, their taxonomy is relatively well articulated, and their field identification is made tractable by numerous museum collections and field guides. In particular, the vocal behavior of birds makes them highly detectable in the field, and accurate guides to the sounds of Amazonian bird species are becoming increasingly available. Bird species ranges have also been described in more detail than those of other Amazonian taxa, and up-to-date range maps (e.g., Schulenberg et al. 2006, Schulenberg et al. 2007, Ridgely and Tudor 2009) are potentially useful for tests of some hypotheses concerning the effects of regional differences and dispersal limitation.

Modeling framework

I used multiple regression and ordination approaches to evaluate the relative influences of multiple factors on bird community composition by collecting and comparing standardized survey data on plant and bird species occurrence at numerous locations where environmental conditions, human influences, and distances among sites were also measured (Gentry 1990, Peres 2000b, Condit et al. 2002). Locations were arranged in an experimental design that recognized a priori observed and hypothesized environmental and biogeographic differences among areas, so that tests of the influence of those differences on avian community distributions would be maximally robust, an approach that partly follows a gradsect sampling philosophy (Austin and Heyligers 1989, Margules et al. 2002). Figure 3.1 displays the study sites in terms of the variables used in their systematic selection.

Sampling therefore occurred across the Amazon River, the boundary between two continental-scale biogeographic regions. Within those two regions, sampling occurred in areas with different plant communities and topography, which in turn reflect different fluvial histories and soil types (Kalliola et al. 1992, Räsänen et al. 1992, Räsänen et al. 1998). Some sites were closer to the city of Iquitos than others, and at a more local scale, some sites were closer to the nearest human settlement than others. Some paired sites were located relatively close to one another, but separated by forest type gradients or regional boundaries, to facilitate the detection of environmental and regional effects independent of distance effects. Table 3.1 lists all of the explanatory variables of interest,

grouped into broad-scale biogeographic factors, local environmental factors, and human factors.

Study Area

The sites where I collected bird survey data were widely scattered within central Loreto Department, Peru, where they were concentrated near Loreto's capitol city of Iquitos (Fig. 3.1). Loreto contains a very high degree of natural landscape heterogeneity, dominated by large areas of terra firme (non-flooded) forest that are dissected along many river courses by linear strands of várzea (seasonally flooded) forest (Marengo 1998). Although várzea forests are generally more extensive in the western Amazon basin than in the east, it has been estimated that only about 12% of the Peruvian Amazon is seasonally inundated (Salo et al. 1986, Kalliola et al. 1992, Toivonen et al. 2007). Similarly, while small-scale forest clearance is common, and is extensive in densely populated areas, cleared areas and secondary forests occupy a small percentage of the total terra firme area at a regional scale (Romero and Ortiz 1998). I limited my research to mature, terra firme forests, the most extensive land cover category in the region, with the hope of adding other habitats in future work.

Four distinctive ecoregions, potentially corresponding to major biogeographic zones, have been delimited in the Iquitos area by the World Wildlife Fund (Dinerstein et al. 1995). The Amazon River divides the Southwest Amazon Moist Forest ecoregion to

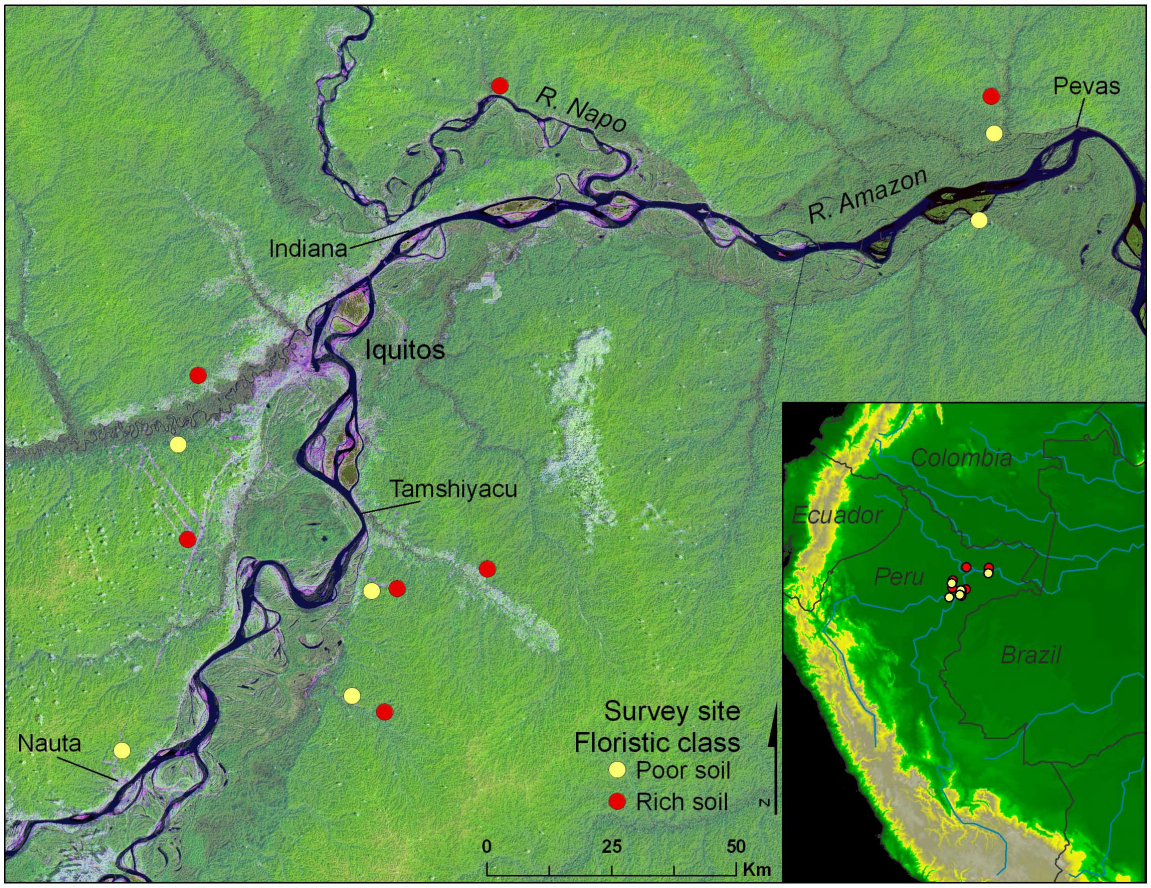


Figure 3.1. Thirteen survey sites were selected with the goal of sampling two general forest types, defined by floristic classes, in two regions. The northern and southern regions were separated by the Amazon River. The poor soil and rich soil floristic classes refer to Pteridophyte and Melastome species compositions typical of forests growing on nutrient-poor, sandy soils, and those growing on nutrient-rich, clayey soils, respectively. Additional goals were to sample sites near and far from Iquitos and from deforested areas. Recently cleared and regenerating forest areas appear as light-colored swaths bordering rivers near Iquitos (the large, light-colored patch in the center of the map is a cloud). The map was prepared from a Landsat mosaic and Space Shuttle Radar Topography Mission (SRTM) elevation data.

the south from both the Napo Moist Forest ecoregion, west of the Napo River, and the Solimoes-Japura Moist Forest ecoregion, east of the Napo. Separating these is the Iquitos Várzea ecoregion, corresponding to seasonally inundated forests within the floodplains of the major rivers. While the regions to the north and south of the Amazon River are widely recognized, the importance of the Napo River as a biogeographic boundary is less clear (Bates et al. 1998, Hall and Harvey 2002, Schulman et al. 2007). In general, it is clear that many avian distributional limits occur at riverine boundaries in the Amazon basin, but whether or not that turnover surpasses normal turnover rates across continuous expanses of forest within ecoregions is less clear (Cracraft and Prum 1988, Schulman et al. 2007).

BIOGEOGRAPHIC HYPOTHESES

Regional biogeography

I focused on the influence of the Amazon River as the primary regional boundary in central Loreto, treating both sides of the Napo River as the same region, and examining only terra firme forests to the north and south of the Amazon River's várzea floodplain. This simplified regional distinction follows, for example, Da Silva et al. (2005). I divided my study sites between those two regions, to the extent possible.

Because biogeographic differences among Amazonian regions are usually considered to be a reflection of species and subspecies distribution limits, I also directly assessed the influence of distributional limits on community composition by coding each

survey site as inside or outside the known range of each species in the survey dataset. Detailed range maps have recently been generated for all Peruvian bird species, representing the best available synthesis of occurrence records for the country (Schulenberg et al. 2006). If regional differences are primarily a result of distributional limits, then those limits themselves should explain more variability in community composition than do regional distinctions. Alternatively, variability associated with species distributional limits can be statistically controlled, and any residual association with regional boundaries can be quantified.

Variation associated with regions, but not with species distributional limits, could arise from species whose distributions cross regional boundaries but whose abundances vary between regions, perhaps due to habitat quality differences, competitive interactions with other species only present in one region, or subspecific disjunctions between regions wherein the two subspecies differ ecologically. To explore these possibilities, I conducted additional tests of regional compositional difference using only those species whose ranges are known to include all of the study site locations.

I also quantified local environmental factors at each survey site, and tested for differences in those factors between the two regions. Regional differences in bird communities may simply be due to environmental differences between regions, so that locally measured environmental factors are all that is needed to explain regional community differences. This is usually not the case, however, and I expected that some combination of local environmental factors and regional geographic distinctions would more fully account for community composition differences among sites.

Community composition analyses at the subspecific level were precluded by the difficulty (impossibility, in many cases) of distinguishing cryptic Amazonian subspecies in the field, but the possibility of subspecific ecological differences is nonetheless of considerable interest. An association between regional abundance differences and regional environmental differences would strengthen the idea that environmental conditions, rather than evolutionary history, are driving regional community distinctions. On the other hand, if species abundances vary across regions despite a lack of measurable environmental difference, and subspecific limits are concordant with those abundance differences, then the idea that the habitat associations of subspecies have diverged over time, and more generally that historical factors partly explain community differences, would be supported.

Despite the many subspecies which are not readily identified in the field, a number of species nonetheless are comprised of subspecies with distinctive vocalizations, plumages, or both, and museum collections are adequate in many other cases for determining the geographic limits of subspecies. While there remains a portion of the Loreto avifauna for which subspecies limits are simply not well described, most wide-ranging species in my dataset could be classified as either having a described subspecies disjunction at the Amazon River in the Iquitos region, or not. It could therefore be asked whether or not species with abundance differences between regions tended to be those comprised of described subspecies that replace one another between regions. Note that while inaccurate and incomplete taxonomic and distributional information can obscure relationships between taxonomy and ecology, this comparison is not absolutely

dependent upon fully accurate taxonomic and distributional information. Rather, a positive relationship at the community level between subspecific disparity and ecological disparity would indicate that currently existing taxonomic and distributional information, although highly imperfect, is nonetheless meaningful with respect to differences among populations and regions.

I classified species with regard to subspecific limits using standard references (Peters 1931-1987, Del Hoyo et al. 1992-2008, Dickinson 2003, Schulenberg et al. 2007). Peters (1931-1987) was used as the baseline subspecific taxonomy, and was updated with more recent information when, and only when, the source was specific with regard to limits at the Amazon River in the study region. In cases where references were silent, contradictory, or otherwise confusing with regard to limits along the Amazon River, they were supplemented by consultation with experts familiar with museum collections from the region. In addition, revisions to the status of subspecies within particular species and genera have been the subject of recent isolated studies, and in those cases the relevant published literature was used to update the Peters baseline. Thus, the subspecific taxonomy used here represents a fairly non-conservative approach to utilizing available and recent information.

Community differences in regional and species-distributional contexts are also likely to be correlated with geographic distance. It was therefore necessary to control for geographic distance both through study site placement (Fig. 3.1), and statistically. Site locations were limited by accessibility and by the availability of existing plant survey data, but I was nonetheless able to select sites near one another on opposing sides of the

Amazon River várzea belt. Many between-region site pairs were therefore nearer one another than many within-region pairs, but correlation between regions and distance could not be discounted entirely. Tests for correlation between community composition and sites' regional situation therefore included geographic distance as a third, controlled variable.

A second approach to testing the relationship between regional differences and geographic distances was also taken, in order to more explicitly address the idea that dispersal limitation can account for regional differences. Geographic distance, or its natural logarithm, is frequently used as a proxy for dispersal limitation, but it contains no explicit information about the potential role of dispersal barriers such as rivers. This is problematic because the regional hypothesis specifically (in the western Amazon basin) implicates rivers as dispersal barriers. If rivers have acted as barriers, then dispersal across rivers should be more difficult than dispersal across expanses of terra firme forest, given similar distances. To simulate this effect, I created a modified distance variable that increased the effective dispersal distance between site pairs when the regional boundary (the Amazon River) fell between them. It was not, however, possible to assign a specific value to the cost associated with a river crossing on the basis of *a priori* knowledge of dispersal limitation in birds. This was due to the nearly complete lack of empirical information regarding the dispersal behavior of western Amazonian birds, and to the fact that many species, probably with widely divergent dispersal behaviors, are treated summarily at the community level. I therefore took an iterative approach, testing a

continuous range of values, in an effort to find the particular value most highly correlated with community differences among sites.

Local environmental factors

Distinctive types of Amazonian terra firme forest are typically defined on the basis of soils, topography and plant physiognomy, and additional distinctions have been made on the basis of floristic differences (Kalliola and Paitan 1998, Schulman et al. 2007, see Chapter 1). Those four factors often co-vary across landscapes, collectively helping to define such formations as white sands forests, sandy-hilly forests, and palm swamps. However, their correlation may be weaker or more difficult to discern in most terra firme, where forests on different soil types may have quite similar physical structures.

The primary soil types of lowland Loreto include extensive ancient lake-bed clay deposits; small, isolated areas of extremely sand-rich soils; belts adjacent to river courses of more recent sandy deposits; and additional tentative distinctions (Räsänen et al. 1998). Soil types are associated with historical deposition events that in turn arose from major geomorphologic processes including the Andean orogeny and the resulting re-direction of major river courses, as well as more recent Andean erosion (Hoorn 1994, Hoorn et al. 1995, see Chapter 1, Hoorn 1996, 2006a). This study focused on distinctions between relatively clayey, nutrient-rich soils usually associated with the Pebas formation, and relatively sandy, nutrient-poor soils associated with near-river terraces of probable Pleistocene origin (Räsänen et al. 1998, Fine et al. 2005). Soil characteristics were only expected to correlate with bird species composition insomuch as they influence plant

communities, which in turn influence bird communities. Correlations between soils and bird communities were therefore expected to be weaker than those between plant and bird communities. However, soils may still serve as efficient indicators of bird community distinctiveness.

Most of the western Amazon is low in elevation and flat at large spatial scales, but local topography can be quite variable, within the limited range of just a few hundred meters above sea level. In general, terra firme tends to be hilly, and várzea floodplains are extremely flat. Soil moisture varies greatly with topography, and this can be related to local plant species composition (Vormisto et al. 2000, Valencia et al. 2004). Topographic complexity has been correlated with avian and mammal species richness at multiple spatial scales, but has usually been measured at regional to continental scales (Kerr and Packer 1997, Rahbek and Graves 2001, Rompre et al. 2007). I used remotely sensed topography data from the Shuttle Radar Topography Mission (SRTM; USGS 2004) to estimate local variability in elevation around survey transects, at four spatial scales, using both elevation range and variance as estimators of variability. In the Iquitos region, high topographic variability is normally equivalent to 'hilliness'.

Vegetation characteristics are among the most important environmental features for birds, and variability in Amazonian plant communities is expected to affect bird species composition. However, plant alpha-diversity is higher in the western Amazon than anywhere else in the world, and taxonomically complete surveys are exceedingly difficult, and have seldom been attempted (Schulman et al. 2007). The ability of a few taxa to serve as reasonable indicators of more general species turnover has been

established in a few cases, and these taxa may therefore be useful for relating species turnover in plants to that in animals. In particular, Pteridophytes (ferns and allies; Photo 3.1) and Melastomataceae (a widespread tropical family whose Amazonian members are comprised mostly of understory shrubs and small trees; Photo 3.2) have been shown to be good indicators of species turnover in canopy trees (Ruokolainen et al. 1997, Ruokolainen et al. 2007). I therefore located bird survey sites over pre-existing Pteridophyte and Melastome survey transects in order to test hypotheses concerning correlations between plant and bird community compositional change.

It is important to distinguish between plant floristics and physiognomy, which, while often spatially correlated, may affect bird communities differently (Rotenberry 1985, Gillespie and Walter 2001, Fleishman et al. 2003, Jayapal et al. 2009). I attempted to quantify physiognomic variation among survey sites by sampling tree diameters, tree stand densities, and leaf litter depths along survey transects, and by measuring the proportion of transects in treefall gap conditions. An additional forest structural measurement at the landscape scale was the degree of forest fragmentation around the surveyed forests, which is described in the following section.

Human factors

Iquitos is the largest city in the Peruvian Amazon, and the surrounding region is undergoing development of urban, agricultural, forestry, and conservation landscapes. The need for geographic information to inform development planning in the region has been stressed by Peruvian governmental organizations as well as non-governmental

Photo 3.1. Species composition of the ferns and their allies (Pteridophytes), along with that of the Melastomataceae, was used to represent species composition of mature forest plant composition more broadly. While direct interaction between ferns and most bird species is limited, fern species composition is quite sensitive to edaphic properties that also affect other plants.

Photo 3.2. Species composition of the Melastomataceae, along with that of the Pteridophytes, was used to represent species composition of mature forest plant composition more broadly. The distinctive leaf venation pattern of Melastomes can be seen here.

organizations (BIODAMAZ 2001, Mäki 2003, Salo and Toivonen 2009, SERNANP 2009). There were two principle human influences of interest for this study: hunting intensity and proximity to areas where primary forest had been recently removed.

Investigating the exact ecological mechanisms whereby those factors may influence species composition and abundances requires a level of detail that I did not attempt in this study; rather, I used a few readily measured indices whose predictive ability could be tested in a modeling framework. As a result, the indices may reflect a combination of human influences that cannot herein be analytically separated. In particular, the accessibility indices used as surrogates for direct measures of hunting intensity may also reflect the influence of other extractive activities that directly or indirectly affect wild bird populations.

Game bird hunting in the Iquitos area appears to be primarily a subsistence activity, but some meat is also brought to markets in the city (personal obs.). As the populations of Iquitos and the surrounding countryside have increased, so has the intensiveness and extensiveness of hunting pressure (Alvarez 2007). Commonly hunted terra-firme game birds in the western Amazon basin include large-bodied members of the families Tinamidae, Odontophoridae, Cracidae, and Psophiidae (Peres 2000b, Peres and Lake 2003). Hunting for the pet trade is by definition commercial, and in the Iquitos area it usually involves members of Psittacidae, the parrot family (Alvarez 2007). Hunting intensity can depend on a site's proximity to human habitations at the local scale, and on its proximity to urban markets at the regional scale (Sierra 1998, Peres and Lake 2003). These accessibility effects can be studied by measuring distances and travel times from

survey sites to local settlements via trails and rivers, and to urban centers via river or road. I considered five relevant urban markets in the study area: Iquitos, and the smaller towns of Tamshiyacu, Nauta, Pevas, and Indiana, all situated along the main stem of the Amazon River (Fig. 3.1). The sizes of local communities, reflecting the number of men potentially involved in hunting activities, may also be important.

Outside of the immediate perimeter of Iquitos, forest conversion consists primarily of clearing around rivers for small-scale agriculture, with additional clearing occurring around the very few roads in the region (Romero and Ortiz 1998, Mäki 2003). Settlements occur near rivers because they are the primary means of transport, and in places where settlement density is relatively high, large contiguous tracts along rivers can exist as a patchwork of agricultural fields in various stages of use or secondary forest regeneration (Pacheco et al. 1998, Romero and Ortiz 1998). Secondary forests are often actively managed agroforests, despite their unkempt appearance (e.g., Padoch and Pinedo-Vasquez 2006). Such areas constitute a distinctive wildlife habitat, and species composition is different than that in adjacent forests (Andrade and Rubio-Torgler 1994, Aleixo 1999, Borges and Stouffer 1999, Naughton-Treves 2002, Naughton-Treves et al. 2003).

Bird species assemblages in forests near agricultural areas may be subsidized with species primarily found in agricultural and edge habitats; this may be particularly true for forest openings such as large treefall gaps, and for the upper forest canopy (Naka 2004). Compositional change can also result from the loss of forest interior species in fragmented forest (Pearman 2002, Laurance 2004, 2006).

In addition to measuring distances between survey transects and the nearest cleared areas and secondary forests, I measured the prevalence of those land cover types in the landscapes surrounding transects, using remotely sensed Landsat imagery in a GIS. Recently cleared areas and young, regenerating forests can be difficult to distinguish from one another, and can be closely intermixed in Amazonian landscapes, so I did not attempt to classify them separately. However, both are readily distinguished from mature forest. I therefore classified land cover as either primary forest or agricultural land, by means of visual image interpretation and validation with GPS ground truth data. I then measured the proportion of each class, the total length of primary forest edge, and the ratio of forest edge to area within four radii around survey transects (Figs. 4.3 and 4.4).

Species Richness

It is well known that, in addition to species and genus composition, species richness, or the number of species found in a place, can also covary with environmental parameters (reviewed, for example, in Hawkins et al. 2003). With regard to species diversity more generally, there are well-established reasons why simple species richness may be less interesting and ecologically informative than a measure of diversity that also incorporates evenness, or the relative commonness and rarity of the various species in a given community (Schluter and Ricklefs 1993). High numbers of species may be ecologically unimportant if most species are rare in a community that is dominated by a few common species. Regardless, due to an important limitation of bird survey data, I only examined species richness. With the exception of the few very common species for which I was

able to perform Distance Sampling (see below), I was not able to account for among-species differences in detectability. While such an accounting is not likely to strongly affect among-site comparisons of relative abundance within species, it is likely to affect among-species comparisons within sites (Buckland et al. 2001). Therefore, since evenness is a measure of relative abundances among species within a community, I did not attempt to estimate it. In practice, species richness is often closely interrelated with measures of diversity that include evenness (Schluter and Ricklefs 1993).

Topographic diversity has been correlated with species richness, including that of plant species in the western Amazon (Tuomisto et al. 2002, Tuomisto et al. 2003b). Hilliness may produce a range of habitats in a small area, particularly due to differences in drainage, soils, and wind exposure between ridges, slopes, and valleys. Many bird species are responsive to those local habitat differences, so that a survey of a topographically diverse area may be expected to result in the detection of more species than would a survey of a relatively flat area.

Animal species richness is also often correlated with plant species richness, but whether animal diversity actually depends on plant diversity is controversial. While a causal ecological relationship almost certainly exists at local spatial scales, the correlations that have been observed at regional and continental scales may be better explained as incidental, having arisen independently from similar responses to climatic gradients or historical factors (Hawkins et al. 2003, Hawkins and Pausas 2004, Rahbek et al. 2007). In the few regional-scale cases in which multiple environmental gradients were measured, plant richness could not explain additional variation in vertebrate richness

once climatic variables were taken into account, whereas plant productivity sometimes could (Boone and Krohn 2000, Hawkins and Porter 2003, Hawkins and Pausas 2004). Nonetheless, it would be useful to know whether or not either Amazonian plant species richness or productivity is correlated with, and therefore possibly predictive of, bird species richness.

Both plant species richness and productivity depend partly on edaphic characteristics. There is evidence that under relatively nutrient-poor edaphic conditions, Amazonian terra firme plant species richness increases with increasing soil nutrient concentrations, whereas at higher concentrations, continued increases in nutrients are associated with lowered species richness (Tuomisto et al. 2002, Tuomisto et al. 2003b). This proposed unimodal relationship accords with a number of studies of the relationship between species richness and 'productivity', in which productivity has nearly always been estimated with an environmental proxy such as nutrient availability, precipitation, or water depth (Rosenzweig and Abramsky 1993, Wright et al. 1993, Pausas and Austin 2001). In the Amazonian case, as in others, the actual relationship between species richness, productivity, and environmental limiting factors may be more complex, because plant abundance (perhaps a more direct measure of productivity) also appears to decline at the highest soil nutrient concentrations (Tuomisto et al. 2002).

Sääksjärvi et al. (2006) found limited evidence for a positive relationship between plant and parasitoid wasp species richness in the Peruvian Amazon at medium spatial scales—but this relationship has otherwise seldom been studied for Amazonian fauna. Amazonian terra firme forest habitats with the most nutrient-poor growing conditions,

which typically grow on white-sand soils, have species-poor plant communities and probably support fewer total bird species than the surrounding terra firme forests (Borges 2004), but those forests are also quite structurally distinct from other terra firme forests, and bird species richness may be influenced by floristic or plant physiognomic effects, or some combination of those and other factors. I did not examine the extreme case of white-sand forests in this study, but I expected that in general and under less extreme conditions, forests growing on nutrient-poor soils in the Iquitos region would harbor fewer species than those growing on more nutrient-rich soils, and that plant and bird species richness would be positively correlated.

There is a larger body of evidence suggesting that forests in highly anthropogenically fragmented Amazonian landscapes support fewer species than do less fragmented forests (Pearman 2002, Barlow et al. 2006, Stouffer et al. 2006). Studies have mostly occurred in Brazil, and have primarily compared extremely small forest patches in highly fragmented landscapes to unfragmented forest interior. Deforestation near towns and small communities in the western Amazon typically shows a different pattern. Near Iquitos, deforestation due to agricultural activities creates cleared and regenerating forest areas in broad swaths along the lengths of rivers and the few roads in the region, adjacent to the vastly larger areas of terra firme forest further 'inland' from the rivers. Isolated forest patches are uncommon, and overall fragmentation levels are not as high as is seen in some Brazilian Amazonian regions.

Road clearing edges examined by Laurance (2004, 2006) in the Brazilian Amazon may have represented fragmentation patterns similar to those found along roads and

rivers in Peru. In that study, bird species richness and abundance were generally reduced with increasing proximity to road edges, with insectivores showing the strongest effects. The region near Iquitos offers an opportunity to observe comparatively subtle effects of forest area reduction and fragmentation on forest interior bird species richness. In general, I examined associations between variation in species richness and variation in all of the environmental and regional variables that were tested for association with species composition.

TESTS OF BIRD SURVEY EFFICIENCY

Survey intensity abbreviations

Establishing efficient survey methods can benefit from an empirical determination of the minimum time period (intensity or effort) required to collect a dataset that is sufficient for resolving the patterns of interest for a particular study. The resulting minimum dataset can be thought of as a surrogate for a more intensive, larger dataset (Caro and O'Doherty 1999). For example, two survey days' worth of data may be a surrogate for data collected over two survey weeks. The more complete dataset is still only an untested surrogate for an even more complete dataset, but the assumption is that it will yield more accurate estimates than any smaller dataset. The question of interest is as follows: how short can the survey period become before the data no longer contain the same community composition patterns as the largest dataset available?

Examining the most frequently and least frequently detected species also addresses a biogeographic question of interest. Some research has suggested that, in general, the most common species tend to be generalists that occupy most sites and that are widely distributed, whereas rare species tend to be range-restricted habitat specialists. It might therefore be expected that site-to-site turnover of infrequently detected species is both more pronounced, and more strongly associated with environmental variation, than that of more frequently detected species. Alternatively, there may be little difference between common and rare species in terms of site-to-site turnover, so that the most frequently detected species can act as efficient surrogates for total avian community compositional variation.

Survey analysis methods: distance sampling vs. index counts

The detectability of birds and other wildlife can vary over time and space in accordance with changes in habitat structure, weather, observer skills, seasonally dependant animal behavior, and other factors. Variable detectabilities across locations or time periods can bias density estimate comparisons, but methods exist for measuring and accounting for the probability of detection (Rosenstock et al. 2002, Norvell et al. 2003). Distance sampling is widely considered a robust means of adjusting density estimates with an empirically derived measure of species detectability (Buckland et al. 2001, Rosenstock et al. 2002, Gale et al. 2009). The combination of timed transect surveys with distance sampling has been shown to produce less biased results than other available methods, with less time investment (Buckland 2006). A recent comparison between intensive

territory mapping and transect surveys demonstrated that distance sampling improves density estimates even in tall evergreen tropical forest, where most detections are by sound and many individuals near the observer probably go undetected (Gale et al. 2009). However, distance sampling is also time consuming and data-intensive, and unadjusted index counts may be preferable when it is not certain that the assumptions and data needs of distance sampling have been met (Johnson 2008). Avian survey datasets in tropical forests usually do not satisfy the sample size requirements for distance sampling at the site level. This is partly because survey sites can be difficult to access, and survey intensities are therefore limited by time constraints. Many tropical species are rare across large areas and will not be detected many times even given high survey intensity. When the goal is to estimate absolute population densities for individual species at particular locations, attempts should be made to overcome these problems and incorporate detectability modeling methods such as distance sampling. However, landscape ecology and biogeography studies normally need to include many sites that may be widely separated, and research questions normally involve relative abundance comparisons among sites. Simple, efficient methods should therefore be preferred if they can be shown to be reasonably good estimators of relative abundance.

I evaluated the utility of simple counts of detections (henceforth referred to as index counts) for relative abundance estimation by comparing results to those obtained using distance sampling to incorporate detectability. For the latter approach, I used DISTANCE, Version 5.0 (Buckland et al. 2001, Buckland et al. 2004, Thomas et al.

2006). Due to the demanding data requirements of distance sampling, I was able to make the comparison for only the 23 most commonly detected species.

Numerical values derived from either index counts or from distance sampling were not taken as accurate estimates of population densities, but rather as indices of relative abundance among survey sites (Johnson 2008). Detection probabilities are normally incorporated in order to derive absolute density estimates, but I did not treat my distance sampling results as such, due to small sample sizes and the clear violation of each of the assumptions required for distance sampling. Furthermore, only relative abundance estimates were required for the comparison of the study sites. The purpose of incorporating detection probabilities was, rather, to avoid the assumption of equal detectabilities within species at different study sites. Detectability may have varied among sites due to subtle vegetation structural differences, differences in the time of year that sites were surveyed, and change over time in my knowledge of cryptic vocalizations. In the latter case, if there were higher numbers of detections of a particular species at sites surveyed later in the term of the project, they could have been a result of increased knowledge, resulting in higher detectability. This bias can, in theory, be corrected for with site-specific adjustments based on empirically derived detection probabilities.

Chapter Four

Data Collection and Analysis Methods

SURVEYS

Sampling Design

I visited 13 sites from 2005 to 2007, spending roughly two weeks at each site including travel time. The bird survey sites, with one exception, were selected from among 43 existing plant survey sites near Iquitos. Selection was guided primarily by the need to include sites on both nutrient-rich and nutrient-poor sites, both south and north of the Amazon River. Secondary criteria were to include sites both near and far from locally deforested and/or populated areas, which were usually coextensive, and to include considerable geographic dispersion in both the southern and northern regions. Such dispersion allowed the separation of a potential river effect, or regional effect, from the effect of geographical distances among sites.

The 43 plant survey locations were viewed in a GIS with Landsat satellite imagery in order to select a subset that satisfied these criteria. Also critical in the selection process were the floristic datasets themselves; ordinations of those data were examined graphically to select a range of floristically distinctive sites on both sides of the river. The exception noted above was the Constancia site, where no plant data existed.

Because a site on nutrient-rich soils was desired in the general geographic area south of the Amazon River and east of the Tamshiyacu River, where no such site existed in the floristic dataset, satellite imagery and the knowledge of botanists who had worked in the area were used to locate that site, and new plant data were collected. Once a site was selected, the bird survey transects were located as near as possible to the plant transect, usually overlapping it, but sometimes a few hundred meters distant. They were only separated when small-scale agricultural clearing during the time between the plant survey and the bird survey made it necessary to adjust the location to remain inside mature forest.

Exploratory and preparatory field work

I spent June 1 to August 12, 2004 at initial study sites 25 to 75 km south of Iquitos. My primary goals were to explore potential study sites, to become familiar with the avifauna, and to develop a bird survey method that could be used at all sites in future field seasons. I also established working relationships with researchers at IIAP, students at the National University of the Peruvian Amazon (UNAP) who accompanied me on field expeditions, and local field assistants.

I made hundreds of individual sound recordings containing thousands of vocalizations for species identification purposes, and after an initial learning period, I established two transects and conducted 14 daily surveys at the San Pedro site. The site was surveyed again in 2005, after I had gained additional field identification skills, and the 2005 data were used in all final analyses. A comparison of the 2004 and 2005 San

Pedro datasets was used to grossly measure the possible contributions of annual variability and surveyor experience to overall variability among survey datasets.

July 15 to September 1, 2005 were also dedicated to familiarizing myself with the avifauna, recording vocalizations, and developing field identification skills, primarily on the north side of the Amazon River. Five survey sites were then sampled in 2005, after which an additional truncation of the number of survey days spent at each site was determined, as described in the following section.

Bird Surveys

The structure of tropical bird communities in general, and Amazonian communities in particular, is notoriously difficult to determine. However, timed transect surveys, during which birds are identified to species visually and by vocalization, are effective for comparing the relative abundances of species among sites (Buckland et al. 2001, Rosenstock et al. 2002, Buckland 2006) and have been used in Amazonian forests (Canaday 2001, Angehr et al. 2002, Rosenstock et al. 2002, Woltmann 2003). I preferred transects to point counts for this study because transects allow very long periods of observation time and therefore increase the probability of detecting the many rare species that typically occur at Amazonian sites, as well as those more common species that are difficult to detect for other reasons. Relative abundances of individual species were estimated with the simple number of detections at each site, as well as using Program Distance, which provides a means of accounting for differences in detectability among sites (Buckland et al. 2001, Buckland et al. 2004). These two relative abundance

estimation approaches were systematically compared for the 25 most common species, as described in chapter five. I followed the avian classification and nomenclature of the South American Classification Committee (SACC) of the American Ornithologists' Union for all decisions concerning the grouping of observations into species and genera, using the most recent revisions up to 2007 (SACC 2007).

The survey sites consisted of two parallel, one-km transects, separated by 250m, through mature forest (Photos 4.1, 4.2, 4.3). This design allowed sampling that included small-scale landscape variability—two kilometers of forest trail typically crossed several hills, valleys, and streams, as well as treefall gaps and forest stands of various ages. Each survey lasted approximately six hours, the time required to slowly walk one transect, stopping to record every individual bird detected. Surveys began at first light under the forest canopy (~5:45 AM), and stops were frequently made to observe multi-species flocks and other bird assemblages such as those at army ant swarms and fruiting trees. Surveys of the two separate transects were made on alternating days, and the direction walked was alternated between days on the same transect.

I recorded the time of each observation, the transect section to the nearest 50m, the distance and bearing to the bird at first detection (estimated to the nearest meter), whether the bird was obviously flocking, whether it was first detected by sight or sound, whether it was perched at some point or only flew over the canopy, and any other relevant notes. In the case of species that typically occur in groups larger than pairs and their young (i.e., monospecific flocks, or monospecific groups within mixed flocks), flock size was recorded as the maximum number of which I could be conservatively sure.

Photo 4.1. Local field assistants helped establish 1 km transects through mature forest, using machetes to clear a narrow path through the understory. Here two members of a community on the Yaguasyacu River in eastern Loreto stop to sharpen their machetes.

Photo 4.2. A typical view along a bird survey transect through mature, terra firme forest in Loreto, Peru. Distances along transects were marked with flagging, and flagged locations were recorded with a GPS.

Photo 4.3. Another typical view along a bird survey transect through terra firme forest in Loreto, Peru. Most of the trees in this view are relatively young, the immediate area probably having only recently regenerated following the disturbance caused by falling trees, which can be seen rotting on the ground.

Stops were made during surveys to record unknown vocalizations and to make voucher recordings for known species. Unidentified audio recordings were identified later in the field, and with reference to commercial audio field guides and my own previous recordings, whenever possible. Bret M. Whitney, a widely recognized expert on Amazonian bird vocalizations, reviewed the remaining unidentified recordings at the end of each field season, while Jose Alonso Alvarez and Juan Diaz of the Institute for Peruvian Amazon Studies (IIAP) sometimes made prior, provisional identifications. Responsibility for the accuracy of all final identifications lies, of course, with the author. I made recordings with a Sennheiser MKH416T shotgun microphone and a Marantz PMD660 digital recorder.

Transects were surveyed six times each at five sites in 2005, for a total of 12 survey days at each site. The resulting data were used to determine that a survey period of eight days was sufficient for describing patterns of species composition similarity among sites. This was done by constructing site similarity matrices with both Sørenson and Steinhaus indices (see analysis methods below) for 12, eight, and four days of data. The Sørenson index uses species presence data only, while the Steinhaus index includes differences in relative abundance among sites. Mantel correlations between all the possible site pair combinations had r-values > 0.94, and were highly significant ($p < 0.001$). Thus, even surveys restricted to four days resulted in datasets containing site similarity patterns very similar to the full datasets. I nonetheless decided to survey sites for eight days, in order to account for particularly rare species that may not have been encountered in the first four days, and to ensure sufficient sample sizes for Distance

Sampling analyses of the most common species. In 2006 and 2007, transects were therefore surveyed four times each, resulting in a total of eight survey days per site.

Each site was visited only once, with the exception of the San Pedro site, which was surveyed preliminarily in 2004. Because surveys occurred across three years, and from late July to early December within years, site comparisons may have been influenced by annual and seasonal variation. I therefore treated year, and Julian day of year, as independent variables and tested for their correlation with avian community composition. A comparison of the two years of survey data at San Pedro was also used to measure annual variability.

Survey data were entered into a Microsoft Access database for storage and organization, and before being exported to statistical software, the data were filtered in the following ways. Only the first eight survey days at each site were included; observations for which the bird(s) were only seen to fly over the canopy without perching were excluded; Neotropical and Austral migrant species were excluded; and observations that could not be identified to species were excluded.

No taxonomic group was systematically excluded from analyses; for example, owls and other nocturnal taxa were included whenever they were observed, even though no special effort was made to adequately survey them at night. Taxa that were clearly not adequately accounted for in this study, due to restrictions imposed by the sampling strategy, include all nocturnal groups, swifts, swallows, and a few small, canopy-restricted hummingbird species. Other rare and difficult-to-observe taxa may have been insufficiently sampled, but the sampling design did not explicitly exclude them.

Species distributions, biogeographic regions, and distance

The bird species distribution maps used in Schulenberg et al. (2007) were made available by Tom Schulenberg at the Field Museum (Schulenberg et al. 2006). Survey site GPS data, River map data, and species distribution map data were all imported to ArcView 3.2 or ArcMap 9.2, and all sites were coded as either inside or outside each region and each species' distribution (Fig.4.1 and 3.1). Only the distributions of those 334 species included in the final survey dataset were included as map data. Species were then treated as binary variables in distance matrices, using the Sørenson index (see below). The region matrix included only one binary variable, with the regions to the north and south of the Amazon River coded as 1 and 0, respectively. Thus, sites covered by the distributions of many of the same bird species were similar, and sites inside the same region were similar. These matrices could then be compared to the bird and plant survey matrices with Mantel tests (see below). Because similarities based on regions and species distributions were likely to be correlated with geographic distance, partial Mantel tests were conducted, using the natural log of geographic distance between sites as the controlled matrix. The natural log of distance is a more theoretically and empirically well-founded measure of dispersal limitation than raw distance, because the decrease in dispersal frequency with increasing distance is not linear (Hubbell 2001, Condit et al. 2002, Ruokolainen and Tuomisto 2002). Geographic distance between all possible site pairs was calculated in ArcMap 9.2 from GPS data.

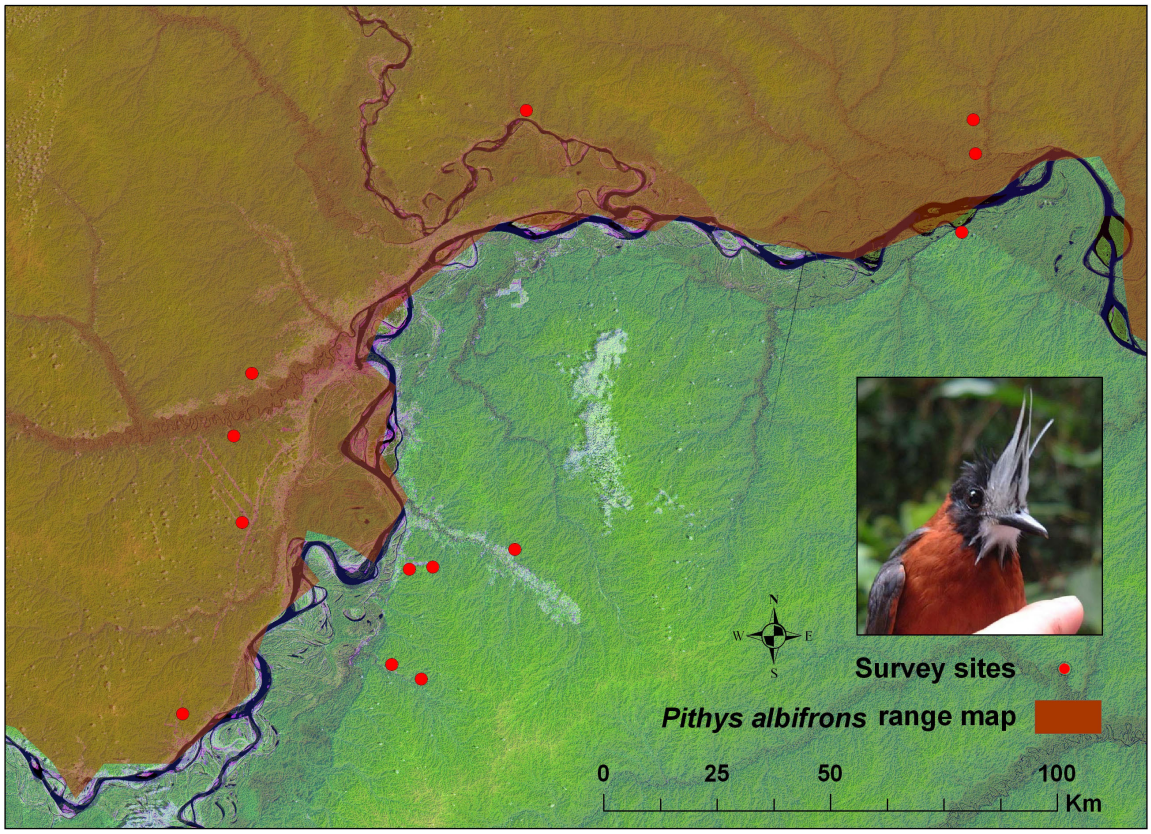


Figure 4.1. Sites were coded as either inside or outside the known distributions of all bird species in the survey dataset, using the most recent and detailed rangemaps available (Schulenberg et al. 2006), to examine the importance for community composition of large-scale distributional factors relative to more local environmental factors. In this example, *Pithys albifrons*, the White-plumed Antbird, is known to have a distributional limit at the Amazon River. As expected, it was observed at several sites north of the river, and at no sites south of the river during this study.

The effect of the Amazon River as a dispersal barrier was examined by multiplying the raw geographic distance matrix by a river barrier coefficient before converting to log distance. If two sites were on the same side of the river, the coefficient was simply 1, whereas if they were on opposite sides, the coefficient was some value greater than 1. Values ranged from 2 to 100 in intervals of 2, and a value of 200 was also included. Thus, the effective dispersal distance was progressively increased in an effort to find the dispersal limitation value that most closely corresponded to the actual community composition differences.

Plant and soil surveys

Existing plant and soil survey data were available through collaboration with members of the Amazon Research Team (ART) at the University of Turku, Finland, who have an extensive network of transects in Loreto. ART surveys were made along five-meter wide, 500-meter long transects within which all individuals of two understory and midstory plant groups (Pteridophytes and Melastomataceae) were identified to species or morphospecies. Methodological details are given in Tuomisto et al. (2003a). Pteridophytes are the ferns and their close relatives, and Melastomataceae is a tropical family comprising many shrub and tree species, most of whose members in the western Amazon are small understory and midstory trees. Between-site species turnover in these groups has been shown to accurately represent total woody plant species turnover at forest sites in Loreto as well as more generally in the western Amazon, and moreover,

they can be identified and counted relatively easily and rapidly (Ruokolainen et al. 1997, Higgins and Ruokolainen 2004, Ruokolainen et al. 2007).

Professor Manuel Flores of the National University of the Peruvian Amazon (UNAP) in Iquitos conducted the Constancia plant survey. Professor Flores had worked previously with the ART at other survey sites and was familiar with their data collection protocol. Hanna Tuomisto and K. Ruokolainen later checked the identifications of voucher specimens collected by M. Flores.

Abundance data were available for most sites, but only presence data were available for three sites. All floristic analyses were therefore restricted to plant species presence data. Presence measures of species turnover are very highly correlated with measures that include abundance data for Pteridophytes and Melastomataceae in the western Amazon, and they result in very similar patterns of association with environmental variables (Tuomisto et al. 2003a, Higgins and Ruokolainen 2004).

Soil samples were collected by ART surveyors along the plant survey transects. Three samples were collected for each site, at the extremes and middle of each transect, and values for the three samples were averaged. Collection and processing methods are described in Tuomisto et al. (2003a). Soil variables used here included pH; loss on ignition (LOI, a measure of organic content); particle size measurements including percentages of clay, silt, and sand; and concentrations of Aluminum (Al), Sodium (Na), Calcium (Ca), Potassium (K), and Magnesium (Mg). While anionic Al is toxic to plants at high concentrations, the remaining cations are plant nutrients that are normally found at higher concentrations in clayey, as contrasted with sandy, western Amazonian soils.

For analyses, cation concentrations were examined separately and summed, and clay and silt percentages were summed.

Forest structure measurements

Forest structural measurements were made with a plotless point-quarter method in 100m intervals along transects, so that each site had 22 subsampling locations. Subsamples were placed on a random side of the transect, at a distance of ten meters, to avoid understory clearing near the transect trail. Diameter at breast height (DBH) of the four trees nearest the sample point was measured to the nearest centimeter, their canopy height was visually estimated to the nearest meter, and their distance from the center point was tape-measured. This was done for trees >10cm DBH and for those < 10cm DBH, so that a total of 8 woody stems were sampled. DBH is a frequently used measure of forest structural complexity, and has been correlated to bird habitat use in many situations (e.g., Davenport et al. 2000, Daw and DeStefano 2001, Parolin et al. 2004). DBH measurements were made above any large buttresses. Leaf litter depth on the forest floor was visually estimated to the nearest centimeter by scanning the ground within 5m of the sample point, because many tropical forest bird species are highly dependent on insect prey found in leaf litter. When the depth of the litter was not visually obvious, I dug to the soil surface in several locations. Finally, the understory foliage density was visually estimated within the same 5m circles, on a scale of 0 to 5, considering foliage from the ground to a height of three meters.

Additional forest structure measurements were made along the entire transects. Natural gaps caused by treefalls are common in Amazonian forests, and some bird species avoid them, while others are highly associated with them (e.g., Terborgh 1985). The extent of treefall gaps along transects was estimated by the linear distance of the transect which actually passed through each gap. The frequency of small streams was similarly estimated by frequency of crossing, and the bank-to-bank width of each stream crossing was recorded.

Topographic measurements

All topographic measures were made by overlaying GPS locations of transect points on a Digital Elevation Model (DEM) in a GIS. I used data from the Shuttle Radar Topography Mission (SRTM), downloaded from the United States Geological Survey website (USGS 2004), which has 90 m spatial resolution. The range of elevations in a study area, from lowest to highest, is a useful measure of topographic complexity (Rahbek and Graves 2001, Rompre et al. 2007), but variance in elevation may provide more information about the general hilliness or flatness of an area. I calculated both range and variance directly from the set of DEM pixels included in 0.15, 0.5, 1, and 2 km buffers around the survey transect GPS locations (Fig. 4.2).

Both transects were pooled for a single measure per site, resulting in six estimates (elevation range and variance for three buffer sizes) per site. Due to slightly irregular GPS point locations and varying relationships between the transect directions and the SRTM grid, the number of pixels inside the buffers varied slightly. To ensure that

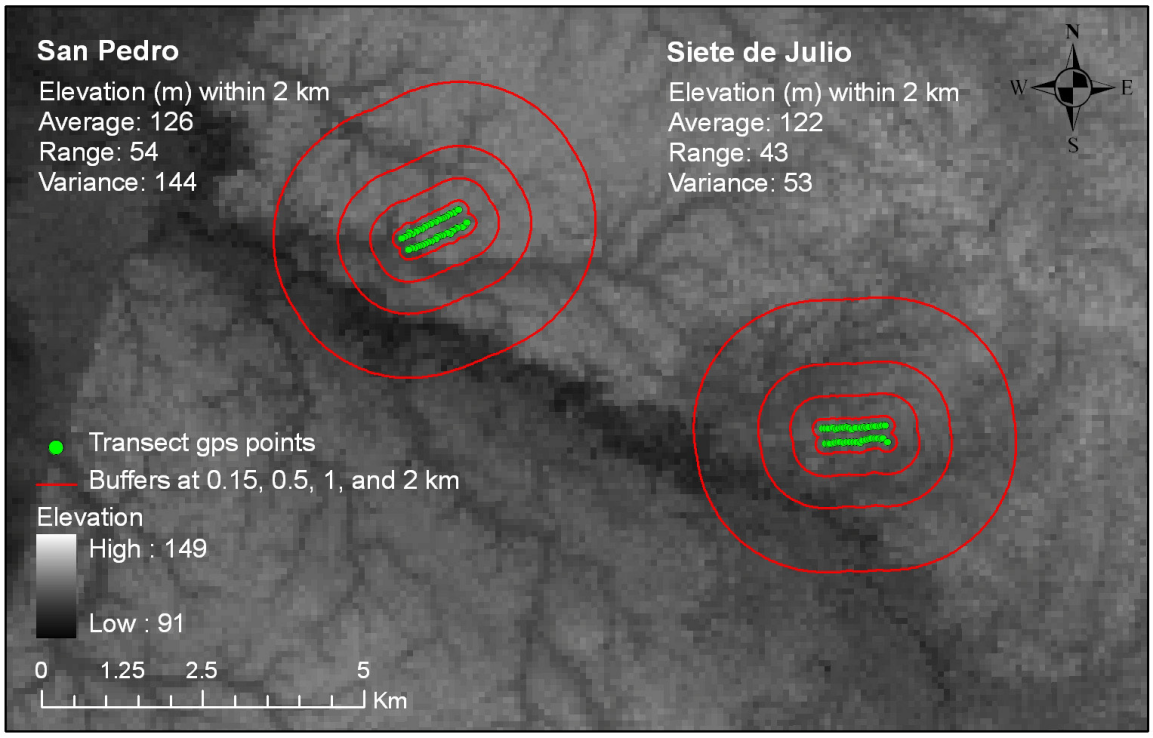


Figure 4.2. A digital elevation model (SRTM, USGS 2004) was used to calculate topographic measures within four radii around avian survey transects. In the two examples shown here, the San Pedro site can be seen to be more locally hilly than the nearby Siete de Julio site, and this is reflected by a higher variance in elevation, despite the two sites' somewhat similar elevation ranges. The contrast between hilly terra firme uplands and adjacent várzea forest is also illustrated by the Amazon River's low, flat floodplain immediately to the west of the San Pedro site. The apparently very low-elevation areas along the small river flowing east to west in the center of the image are partly an artifact of local agricultural clearing. The SRTM data are influenced by forest canopy cover, so that cleared areas appear to be lower in elevation; this undesirable artifact was not corrected for in analyses. Note that within this image, the total elevation range is only 58 meters.

variance was not affected by sample size, a standard sample size was chosen for each buffer size, defined by the site with the smallest number of pixels included. Pixels closest to the periphery of the buffer were excluded at other sites until the standard sample size was reached. This resulted in samples of 75, 261, 672, and 2059 pixels, in order of increasing buffer size.

Measures of agricultural clearing and forest fragmentation

To quantify the prevalence of anthropogenic habitat in landscapes near survey sites, I manually classified the areas within a four kilometer radius of survey transects as either primary forest or agricultural land, where 'agricultural' included open agricultural fields (*chacras*), young secondary forest (*purmas*), and any other non-forest, anthropogenic land cover such as local village centers. Open water was classified separately. Agricultural and other cleared areas are generally highly distinct from mature forest in Landsat TM imagery when a combination of visual and near-infrared bands is displayed, and the human eye can readily be trained to distinguish them accurately. I visually interpreted cloud-free Landsat TM images from the same year that the survey data were collected, using a combination of bands 1, 4 and 5, and digitized forest and agriculture polygons onscreen (Figs. 4.3 and 4.4).

To validate the classification, I also collected GPS data, describing locations in the field as mature forest (63 points), *chacra* (six points), *purma* (16 points), village or other domestic clearing (18 points), or forest/agriculture edge (five points). There were therefore totals of 63 mature forest points, 40 agricultural points, and five

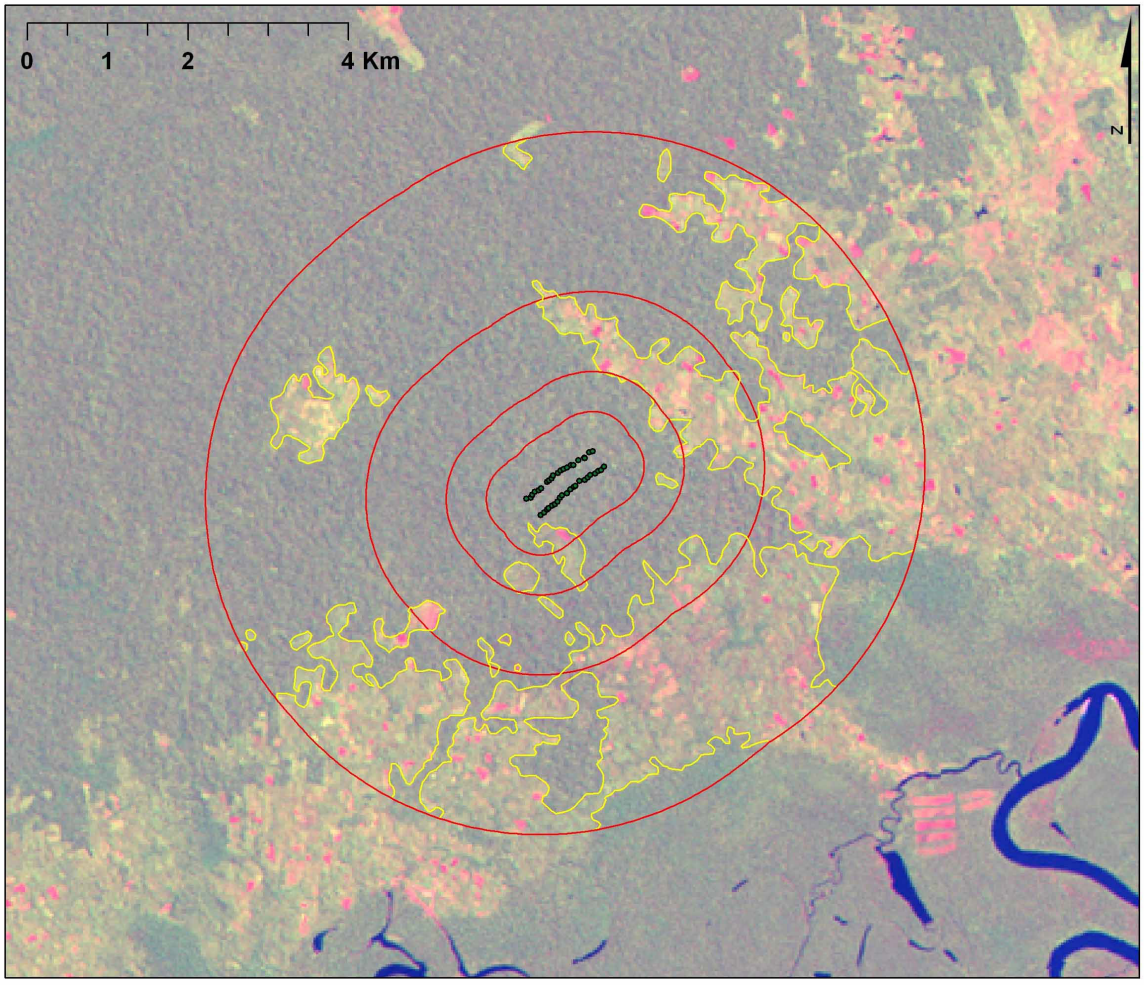


Figure 4.3. Landsat satellite imagery was used to calculate the total area of mature forest and agricultural areas, the length of mature forest edge, and the forest edge-to-area ratio within 0.5, 1, 2, and 4 km radii around bird survey transects. This example shows land cover surrounding the Tarapoto site in the lower Nanay River basin. The two transects are surrounded by buffer circles in red, and digitized forest edge is shown in yellow. Very recently cleared fields (*chacras*) and young regenerating forest (*purma*) appear pink and yellow-green, respectively, with floodplain forest (várzea) to the southeast, and mature upland forest (terra firme) to the northwest. Landsat path 6, row 63, 22 August 2005.

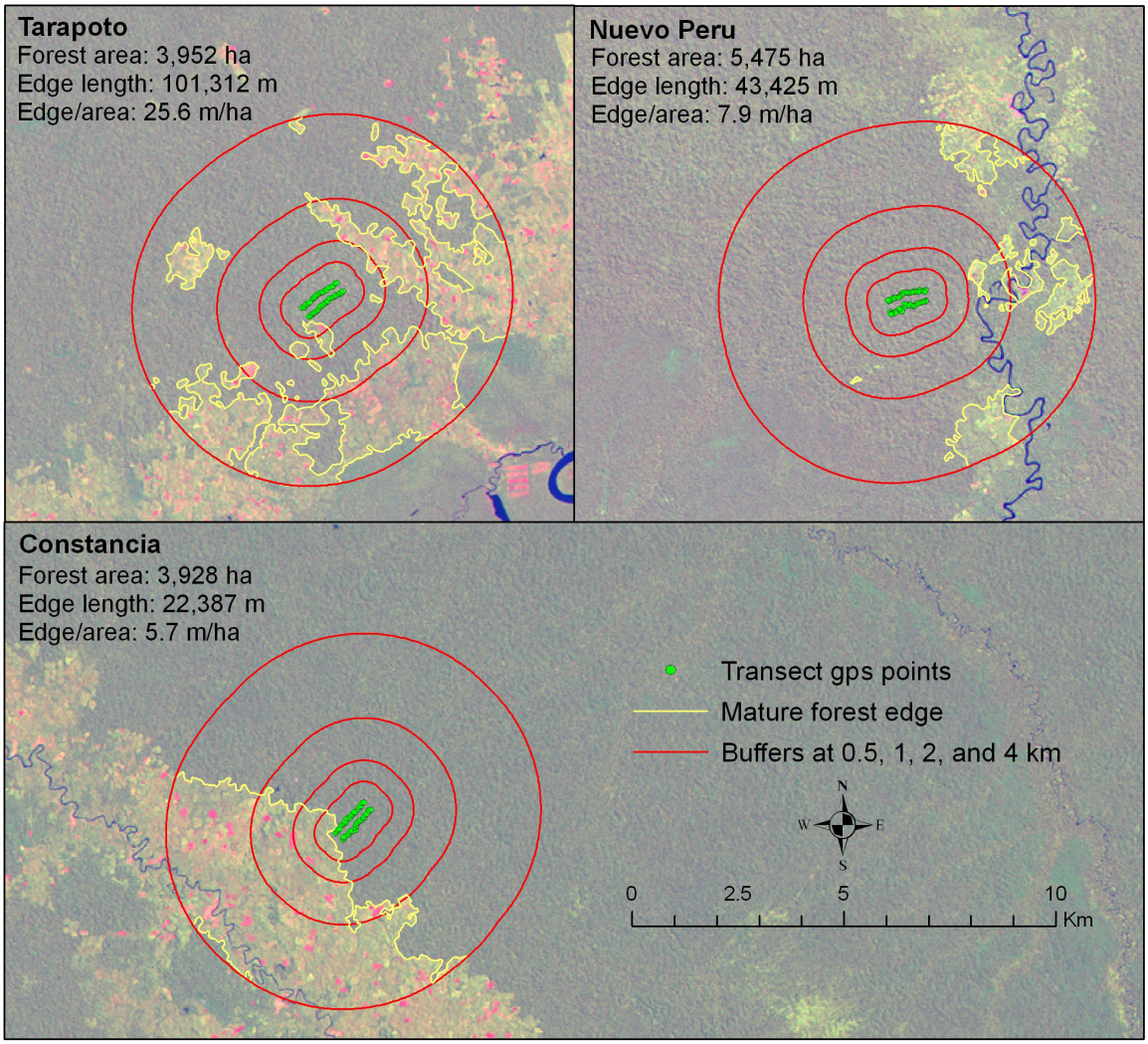


Figure 4.4. These examples of digitized mature forest edge in landscapes surrounding bird survey transects demonstrate the variability among sites in forest cover and fragmentation. Tarapoto was the second most fragmented site, with a large proportion of the area within 4 km of the transects used for shifting agriculture in a pattern that resulted in a high forest edge-to-area ratio. A similar amount of land was used for agriculture near the Constancia transects, but in a more compact pattern that resulted in lower fragmentation and a low edge-to-area ratio. Nuevo Peru had the second smallest amount of recently cleared land near the transects (none within 1 km), and a moderate edge-to-area ratio. See Figure 4.3 for additional details.

forest/agriculture edge points. Edge points can never fall exactly on an edge in a vector classification, so they were considered correctly classified if they fell within 50 meters of a polygon edge, allowing for GPS error and the 30-meter imagery resolution. Only three points were misclassified, all of which were open areas classified as mature forest. Thus, there was an accuracy rate of 97 percent, slightly biased towards underestimation of agricultural area. The unusually high accuracy rate probably resulted from the ease of image interpretation at such a highly general level of distinction between only two classes. It is possible that the misclassified agricultural areas were cleared between the time that the image was collected and the time that the GPS data were collected, even though both datasets would have been collected within the same year. However, in none of those particular cases did I note during my visits that the areas were particularly recently cleared.

Straight-line distances between survey sites and open areas were then measured in a GIS by superimposing transect GPS locations on the land cover classification. I also calculated the area of both cover classes and the length of forest edge within 0.5, 1, 2, and 4 km buffers around transects. Forest edge did not include non-anthropogenic edges such as riverbanks. From those measurements, I derived land cover proportions and forest area-to-edge ratios within each buffer.

Measures of hunting influence

Although hunting intensity can be difficult to measure, it is dependent on site accessibility and can be estimated by measuring the walking distance to the nearest trail

or river, and to human habitations (Peres and Lake 2003). Walking times between a site, the nearest habitation, and the nearest village center were recorded in the field. The associated GPS data were also collected, and straight-line distances were measured in a GIS. Travel distances along rivers or roads between survey sites and urban centers with commercial markets were also measured in a GIS, and estimated travel times using local transportation methods were recorded in the field. I identified five relevant urban centers in the study area: Iquitos, and the smaller towns of Tamshiyacu, Nauta, Pevas, and Indiana, all situated along the main stem of the Amazon River.

ANALYSES

Comparative framework

Avian communities were characterized in terms of species composition, genus composition, and species richness. Two measures of composition were employed at both taxonomic levels: one that only counts taxa as detected or not detected, and one that incorporates relative abundance information. The measure of relative abundance was simply the number of times a species was detected at a given site.

Resemblance matrices were employed as the fundamental form of data organization to compare sites and to compare among-site community composition differences to environmental and regional variables. Each cell in a resemblance matrix contains a numerical measure of similarity or distance between a particular pair of sites for any variable of interest, and all possible site combinations are represented by a cell.

This format is particularly useful for making comparisons among disparate types of spatial data (Legendre and Legendre 1998, Legendre et al. 2002), and has been used for comparing bird survey data to environmental variables (Rotenberry 1985, Fleishman et al. 2003, Jankowski et al. 2009).

Matrix cells contained Euclidean distance in the case of univariate environmental factors such as geographic distance between sites, elevation, tree basal area, forest fragmentation indices, and soil variables such as individual and summed cation concentrations. The Steinhaus (Bray-Curtis) and Sørenson indices were used to estimate multivariate community composition distance for bird species and genera, plant species, and bird range map information. These two indices are mathematically identical aside from the difference that the Steinhaus index incorporates abundance information, in this case counts of individuals detected, whereas the Sørenson index only uses presence information, essentially a count of one (Legendre and Legendre 1998). Both indices exclude double-zeroes, which are site-site comparisons for which the species in question was not detected at either site. For the sake of consistency, all matrices used in analyses were distance matrices, where higher index values indicated greater distance, or *dis*similarity. Steinhaus and Sørenson index values are often given as similarities, ranging from 0 to 1, where 1 represents identical species composition. These were converted to distance with the formula Distance = 1 – Similarity, so that an index value of 1 was equivalent to complete dissimilarity. Thus, all of the multiple kinds of matrices used in analyses can be interpreted in the same way as those for geographic distance, for which higher cell values indicate greater distance between sites.

For all comparisons of community composition and environmental or regional variables, a resemblance matrix was constructed for each data type, and congruence among matrices (e.g., between forest clearance and bird species composition) was quantified with Mantel tests (Sokal 1979, Legendre and Legendre 1998, McCune et al. 2002, Legendre and Lapointe 2004). The Mantel test was designed to evaluate correlation between resemblance (either distance or similarity) matrices in a manner analogous to a Pearson correlation, but it accounts for non-independence of matrix cells in the estimation of p-values. Mantel r-values are interpreted in the same way as the Pearson correlation coefficient, although the Mantel test tends to result in consistently lower r-values than does Pearson correlation (Legendre and Legendre 1998, McCune et al. 2002).

Bird species and genus composition matrices were then modeled with multiple explanatory matrices, using multiple regression on matrices (Legendre et al. 1994, Legendre and Legendre 1998, Tuomisto and Ruokolainen 2006). Independent variables that were significantly correlated with variation in bird species composition in Mantel tests were included as input variables in multiple regressions, and a stepwise procedure was used to select final model variables. Mantel tests were conducted using pc-ord (McCune and Mefford 1999), and Multiple regressions on matrices were conducted using program Permute! (Casgrain 1998).

Community compositional differences were also visualized with Nonmetric Multidimensional Scaling (NMS), an ordination technique that is suited to ecological community data and that typically results in the reduction of datasets to two or three axes containing most of the variability of the original data (Kruskal 1964, Mather 1976,

Legendre and Legendre 1998, McCune et al. 2002). NMS was performed in pc-ord (McCune and Mefford 1999), using the Steinhaus and Sørenson distance indices, ten runs on the real data from random starting configurations, and using Monte Carlo randomization tests of significance and the degree of stress reduction with increasing dimensionality to select the appropriate number of dimensions for each ordination. NMS ordinations were also performed with the floristic datasets, using the Sørenson index.

Species richness

Species richness was estimated by both the simple count of species detected at each site regardless of sample size differences among sites, and by rarefaction resampling to a standardized sample size, using the software EstimateS, version 8.0 (Colwell 2006). Rarefaction is a widely used method of estimating species richness in ecological datasets that have been sub-sampled to minimize several kinds of sampling bias (Sanders 1968, Simberloff 1978, Gotelli and Colwell 2001). Rarefaction is usually employed to adjust for unequal sampling effort, which was not required in this study, because sampling effort was standardized in terms of time and observer experience. However, total numbers of observations were quite variable among sites, which probably reflected a mixture of real abundance differences and sampling error associated with weather, unpredictable bird movements and vocalization patterns, and other factors. Rarefaction should produce a measure of richness controlling for any such abundance effects.

I examined both simple species counts and rarefaction estimates because while differences in richness that are independent of abundance effects are of theoretical

interest, simple species counts may more accurately indicate the number of species actually present, given standardized sampling effort and real differences in abundance. I made no effort to model species richness as an asymptote extrapolated from a sampling curve (Gotelli and Colwell 2001). The simple species count on a given plot was the number of species detected during the complete sampling period, including all individual observations, the number of which varied considerably across sites. Rarefaction sub-samples were made at increasing sample sizes from five observations to the total sample for each site, at five-sample intervals. I used random sampling of individual observations without replacement, and calculated the average richness estimate from 1000 iterations at each sample size (Gotelli and Colwell 2001, Colwell 2006). For analyses of association between species richness as estimated by rarefaction and environmental variables, I used estimates for the sub-sample of 839 observations per site, because that was the total number of observations at the site with the fewest observations; i.e., the maximum sample size that could be standardized across all sites.

SURVEY ABBREVIATIONS AND DISTANCE SAMPLING

Wide-ranging species subsets

Distributional limits of many species in the dataset occur within the study area, especially at the Amazon River, and study sites were distributed on both sides of the river. A subset of the full species list was therefore created by limiting the species to those whose known distributions covered all 13 survey sites. The resulting 'wide ranging' species dataset was

used in regional analyses to evaluate correspondence between species compositional variation and regions that was not due to species distributional limits.

The wide ranging species subset was also used to improve tests for local environmental correlates of compositional variation. This was done primarily to avoid a sampling artifact: the inclusion of sampling sites outside the range of a given species will increase the number of sites where the species is not detected, regardless of habitat type, decreasing the likelihood of detecting real habitat associations. Sites that satisfy a species' habitat requirements but that are outside its distribution due to dispersal limitation would confound the analysis of local habitat associations.

Distributions are more expansive at the genus level, and particularly when genera included river-restricted species, this often meant that more survey sites fell within the genus distribution than within the species distributions, rendering habitat association tests more powerful at the genus level. The wide ranging species subset, in addition to constituting a better test of environmental associations at the species level, offered a way of producing more equivalent tests at the two taxonomic levels.

Survey intensity abbreviations

Sampling intensity abbreviations were tested by comparing matrices constructed from all bird observations during eight survey days to matrices constructed using fewer survey days. Observations from the eighth, seventh, etc. survey days were sequentially removed to generate seven progressively smaller datasets. The later dates were removed first in order to simulate the actual datasets that would have existed, had the surveys only been

conducted for the limited number of initial days. Matrices were then constructed from the limited datasets using the Sørenson and Steinhaus indices for presence and abundance data, respectively. Those matrices were then compared to the original eight-day resemblance matrices with Mantel tests.

Relative abundance measures: Distance sampling vs. index counts

Sample sizes for individual species at single sites were usually very small (<30) relative to the normal requirements for distance sampling (Buckland et al. 2001). Distance sampling-based detection functions were not developed for species with fewer than ten detections at a majority of sites. A more restrictive cut-off would have excluded all but a small handful of species, rendering the community-level comparison of sampling methods pointless. The comparison is nonetheless useful, because small sample sizes will be the norm for most tropical bird community evaluations.

The incorporation of detection probabilities entails several choices that can affect the resulting relative abundance estimates. Most importantly, detection probabilities can be developed at any level of analysis, from the global level that includes all data from all sites for a given species, to the site level, to finer levels that may, for example, treat males and females separately (Buckland 2006), or treat individual transects as within-site subsamples. However, developing detection probabilities requires a large number of detections, relative to the number usually obtained for rare species, so that dividing datasets into subsamples reduces the number of species for which sufficient data exist, and increases the uncertainty in estimates for the species that are evaluated. I therefore

did not develop detection probabilities for within-site subsamples, even though, given sufficient sample sizes, it would have been useful for comparing among-site variance to within-site variance. Data were instead pooled at the site level for each species, and site-specific detection probabilities were developed for those species for which sufficient data existed.

Twenty-three species were detected more than ten times at each of six or more sites, and of those, only six were detected more than ten times at all 13 sites. Several included species were restricted to sites on one side of the Amazon River, but were abundant at all sites where they were detected. A density of zero was assigned to species at sites where they were not detected. If a species was detected at least once at a site but fewer than ten times, a global detection function for the species across all sites, otherwise calculated in the same way as the site-specific functions, was applied to the data at that site. Normally, this occurred at only one or two sites for a given species.

Detectability modeling procedures followed the recommendations for line transect surveys given by Buckland et al. (2001). Results for all 23 species were obtained using both site-specific detection functions and a global detection function across all sites. In both cases, automated sequential selection in DISTANCE, Version 5.0 (Thomas et al. 2006) was used to fit the best models. Half-normal, uniform, and hazard candidate key functions with cosine adjustments were tested, and various data truncation distances and distance groupings were examined to improve goodness of fit. Akaike's Information Criterion (AIC) was used to select the best models from among those with equal truncation distances.

Distance sampling normally includes spatial sampling design procedures implemented in a GIS which allow the inference of population densities from study sites to surrounding landscapes (Buckland et al. 2001). In this study, the location of study sites was restricted both by the difficulty of accessing most sites of interest, and by the prior location of plant survey sites. Therefore, site selection took place independently of distance sampling design procedures, and no inference of population densities to surrounding landscapes was attempted on the basis of density estimates at survey sites. Rather, the relationships of interest were those between density estimates and index count estimates as alternative measures of relative abundances among sites.

Several Mantel tests of matrix correlation were performed for the comparison of the resulting datasets to index counts. The Steinhaus index of species compositional similarity among sites was used in all cases, because distance sampling estimates are by definition a measure of abundance. Species subsets of index counts were made for the 23 modeled species, and for the remaining species for which detectability was not modeled. Incidentally, Mantel tests between those two resulting groups also constituted a test of correlation between variations in community composition of common vs. rare species. Finally, Mantel tests were also used to evaluate correlations between variation in distance sampling density estimates for the 23 modeled species and the daily survey abbreviations of index counts described above.

Chapter Five

Tests of Bird Survey Efficiency

RESULTS

Distance sampling yielded density estimates that were generally very highly correlated with the index count data for each of the 23 common species considered, and all Pearson correlations had associated p-values below 0.05, even when site-specific density functions were used (Table 5.1). However, correlations ranged to a low of r = 0.56 for *Glyphorhynchus spirurus* and *Thamnophilus murinus* when site-specific density functions were used, and were only slightly higher for a few additional species. Mantel correlations between site matrices constructed from index counts and distance sampling for all 23 species were also very high (r = 0.92, p = 0.0001 using global density functions; r = 0.80, p = 0.0001 using site density functions).

To estimate their ability to represent the remainder of less common species detected during surveys, matrices including the 23 common species were compared to a matrix including index counts for all additional species, but excluding those 23 species. Mantel correlation coefficients were r = 0.77, p = 0.0001; r = 0.74, p = 0.0001; r = 0.62,

Table 5.1. Pearson correlations between relative abundance estimates using index count data and distance sampling. Density estimates were made using density functions (DF) calculated on a site-specific basis, and using data from all sites pooled (global DF). Correlations are across all survey sites (n = 13).

	Site-specific DF		Global DF	
Species	R	P	R	P
Tinamus guttatus	0.80	0.001	0.98	0.0001
Patagioenas plumbea	0.88	0.0001	0.95	0.0001
Trogon viridis	0.77	0.002	1.00	0.0001
Capito auratus	0.85	0.0001	0.99	0.0001
Glyphorhynchus spirurus	0.56	0.048	1.00	0.0001
Xiphorhynchus elegans	0.98	0.0001	1.00	0.0001
Xiphorhynchus guttatus	0.78	0.002	0.95	0.0001
Thamnophilus murinus	0.56	0.048	1.00	0.0001
Thamnomanes saturninus	0.98	0.0001	1.00	0.0001
Myrmotherula axillaris	0.88	0.0001	0.95	0.0001
Zimmerius gracilipes	0.94	0.0001	0.87	0.0001
Lophotriccus vitiosus	0.89	0.0001	1.00	0.0001
Lipaugus vociferans	0.90	0.0001	0.99	0.0001
Tyranneutes stoltzmanni	0.94	0.0001	0.99	0.0001
Lepidothrix coronota	0.65	0.016	0.99	0.0001
Chiroxiphia pareola	0.90	0.0001	0.95	0.0001
Dixiphia pipra	0.97	0.0001	0.99	0.0001
Pipra erythrocephala	0.98	0.0001	0.96	0.0001
Pipra rubrocapilla	0.98	0.0001	1.00	0.0001
Hylophilus hypoxanthus	0.62	0.023	0.76	0.002
Tangara chilensis	0.69	0.009	0.80	0.001
Cacicus cela	0.93	0.0001	0.94	0.0001
Euphonia rufiventris	0.61	0.027	0.90	0.0001

p = 0.0001; for index counts, estimates using global density functions, and those using site-specific density functions, respectively. Thus, those 23 common species were relatively good indicators of species turnover patterns in the remainder of the bird community. Mantel correlations were stronger, as expected, when variation in the 23 most common species was compared to that in the whole 334 species dataset (r = 0.88, p = 0.0001; r = 0.84, p = 0.0001; r = 0.72, p = 0.0001; for index counts, estimates using global density functions, and those using site-specific density functions, respectively). Distance sampling using global density functions performed very similarly to the count data, as expected, whereas the use of site-specific density functions lowered correlation between the species groups.

Survey abbreviations simulating increasingly intensive surveys showed among-site variation in species composition that was extremely similar to the variation in the full eight-day dataset, particularly when relative abundance data were used (Fig. 5.1). Similarity in among-site variation fell off more rapidly with reduced survey intensity for presence-absence data than for abundance data, but even so, the Mantel R-value remained above 0.90 after only four survey days. The amount of new information gained about variation in community composition, per unit of survey effort, was quite small after the fourth or fifth day.

Mantel correlations between variation in abbreviated surveys and variation in the full eight-day surveys for the 23 most common species were also very high (Fig. 5.2). Correlations were weaker than when all 334 species were included, and were weaker when distance sampling estimates were used than when index counts were used. This was

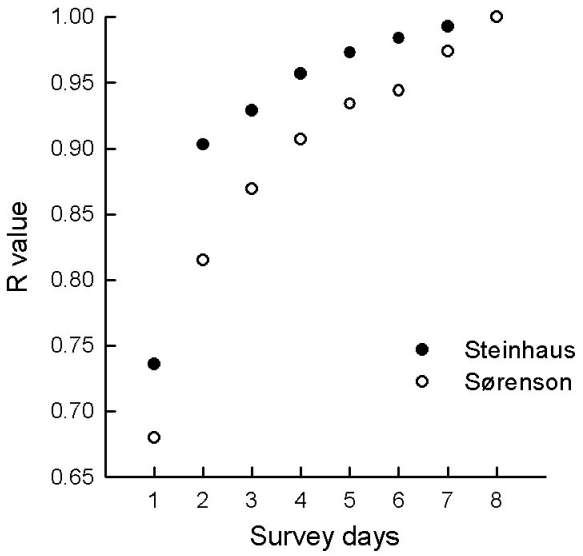


Figure 5.1. Mantel correlations between full eight-day bird surveys and abbreviated surveys, sequentially removing the last survey day, in chronological order. R-values from Mantel tests are shown for each abbreviation, using the Steinhaus index, which incorporates abundance information, and the Sørenson index, which only uses species presence-absence. All associated p-values were less than 0.001. As days are removed, abbreviations using abundance information remain more strongly correlated to the full dataset than do those using presence-absence.

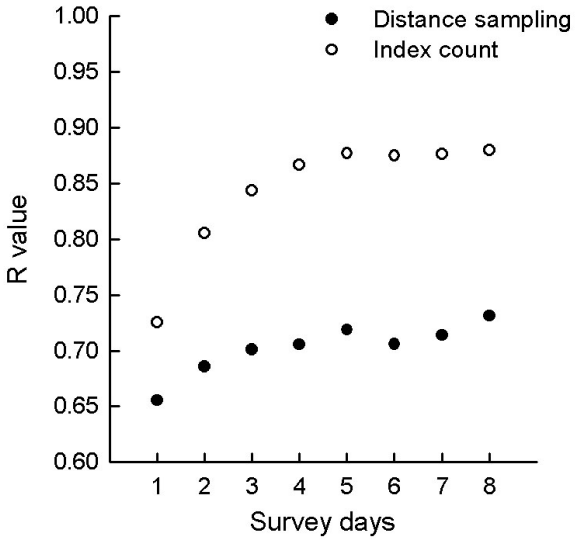


Figure 5.2. Mantel correlations between full eight-day surveys including only the 23 most common species and abbreviated surveys for the entire species dataset. For the full-length surveys using only common species, relative abundance estimates were made using distance sampling, and using only index counts of detections. R-values are shown; all associated p-values were less than 0.001. Variation among plots in the relative abundances of the most common species was very highly correlated with variation in the whole species dataset using either method, even when only a few survey days of the entire species dataset were used.

expected, because the abbreviated surveys only included index counts. Still, the relationship between the abbreviated surveys and the distance sampling abundance estimates was quite strong, but did not significantly improve after the fourth or fifth survey day.

DISCUSSION

Index counts of species observations and density estimates developed using distance sampling yielded extremely similar patterns of variation in relative abundance for the 23 most common species in the survey dataset. This was true for each of the individual species considered, and grouping all 23 species at the community level. However, the relationship between index count estimates and distance sampling estimates was not perfect. If relative abundance estimates using distance sampling with site-specific detection functions are taken to be the least biased estimates available, then the results suggest that simple count data can only be taken as a good surrogate for, not an exact replacement for, results obtained from a more sophisticated and time-intensive analytical method. On the other hand, it is possible that the small sample sizes obtained within single sites for even the most common species led to significant error in the development of detection probabilities, and distance sampling results cannot be taken as necessarily more reliable than the index counts (Johnson 2008).

Researchers wishing to maximize the precision of relative abundance estimates among tropical forest sites are well-advised to use distance sampling, but it will come at the expense of significantly larger time investments at each site. Index counts, on the

other hand, revealed overall relative abundance patterns among sites that were similar to those derived from distance sampling, even when survey intensity was low. Thus, researchers collecting geographically extensive datasets in tropical forest regions where access to sites is limited should have some confidence that index counts are sufficient for revealing biogeographical patterns of interest.

It should be re-emphasized that without comparison to much more intensive estimation methods such as bird banding and territory mapping, the estimation methods that I compared cannot be evaluated with respect to 'true' densities (Johnson 2008, Gale et al. 2009). Therefore, if correlations between community variation and environmental variation were higher when using distance sampling than when using index counts, it could be because the abundance estimates are more accurate, or it may be due to random error. The latter would be statistically unlikely, but it cannot be discounted, and so comparison to environmental variables should not be used as a criterion for the evaluation of the different methods. This impasse is a real one that can only be overcome when densities are estimated with more intensive methods. The finding that results from the two different methods were very similar should, to a degree, obviate the need for such criteria, but there were minor differences that may be of some interest, particularly in cases of individual species. If the relative abundances of many individual species are found to be consistently more strongly correlated with environmental variables when distance sampling is used than when simple counts are used, then the case for using distance sampling even at the community level may be strengthened.

The number of survey days needed to accurately represent community composition patterns was significantly less than the total dataset of eight survey days per site. There may be no objective criteria for deciding how many survey days are sufficient. Rather, the survey intensity required to answer particular research questions should be assessed carefully for any given project or survey area. Ideally, information from previous studies conducted under similar field conditions can be used to inform new field efforts. The results suggest that for community-level biogeography studies in Amazonian forests, four complete survey days may be a sufficient time investment for each study site, given surveyor skills roughly similar to those employed for this study.

Chapter Six

Avian Bioregions Bounded at the Amazon River

RESULTS

Bird community description

A total of 363 species were detected during surveys, but 29 were excluded from analyses either because they were seasonal migrants (12 species), because they were detected only as flyovers (17 species, of which three were also seasonal migrants), or because they were only detected after the initial eight survey days at a site (three species; all surveys after eight days were excluded). 513 observations, of 43 different species, were excluded as flyovers—primarily parrots, raptors, and swifts. The final dataset, including eight survey days at each of 13 sites, comprised 12,913 observations of 334 species, 214 genera, and 45 families (Appendices 1 and 2).

The degree of variation among plots in bird community composition depended on whether relative abundance or presence indices were used, and on the taxonomic resolution considered. However, no two plots were less than 21 percent different or more than 61 percent different by any measure (Figs. 6.1 and 6.2). Community distinctiveness decreased with increasing taxonomic level, with very little among-site variation at the

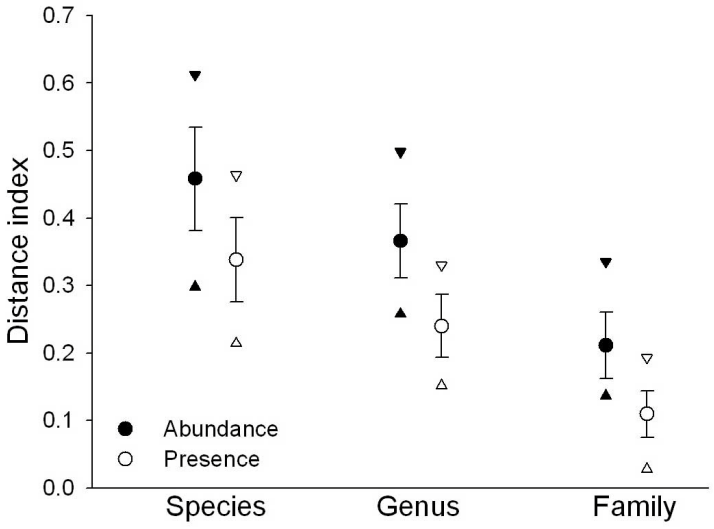


Figure 6.1. Mean (± standard deviation) bird community composition differences among survey site pairs, as measured by the Steinhaus index, which incorporates relative abundance estimates, and the Sørenson index, which uses presence only. Both indices are shown as distances, on a scale of 0.0 (complete similarity) to 1.0 (complete difference). Triangles show minimum and maximum values for both indices. Estimated community distinctiveness clearly increases when abundance information is incorporated, and also increases with increasing taxonomic resolution.

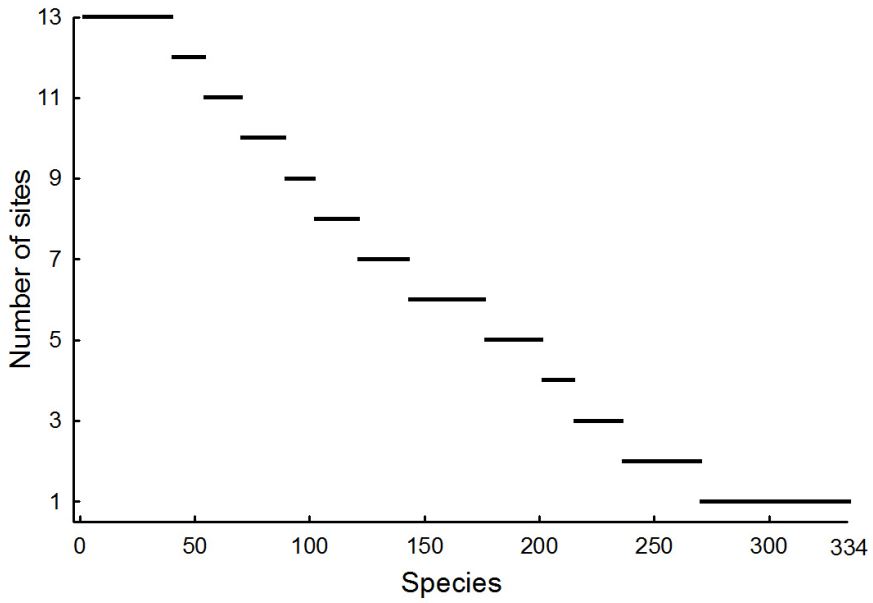


Figure 6.2. Frequency distribution of species presence at 13 study sites. The length of each line corresponds to the number of species that were detected at least once at the indicated number of sites. Thus, 39 of the 334 species included in analyses were detected at all 13 sites, while 65 species were detected at only one site.

family level. Of the 334 species included in analyses, 39 occurred on all plots, 88 occurred on 10 or more plots, 121 occurred on 3 or fewer plots, and 66 occurred on only one plot (Fig. 6.2). Bird communities thus included a large component of widely distributed species that were, at least in terms of presence, generalist with respect to the habitat variables measured and discussed below.

There was, nonetheless, clearly structured compositional variability among plots, as shown by the Nonmetric Multidimensional Scaling results (NMS; Figure 6.3). The plots grouped most strongly into clusters north and south of the Amazon River regardless of distances separating plots, and the plots to the south of the river were more tightly clustered than were those to the north. Those patterns became progressively weaker at the genus and family levels. Among the northern sites, two (Expetroleros and Tarapoto) separated strongly from the others. Those sites showed the highest levels of local deforestation near the survey plots, and indicator species analysis suggested that the species primarily responsible for this pattern were those that responded either positively or negatively to forest fragmentation and proximity to edge habitat. This local effect is discussed in detail in the following chapter.

Site descriptions and timing of surveys

Table 6.1 provides the survey plot names and their abbreviations, which are used in all subsequent results reporting, including tables and graphs. Bird survey dates are also shown for each plot.

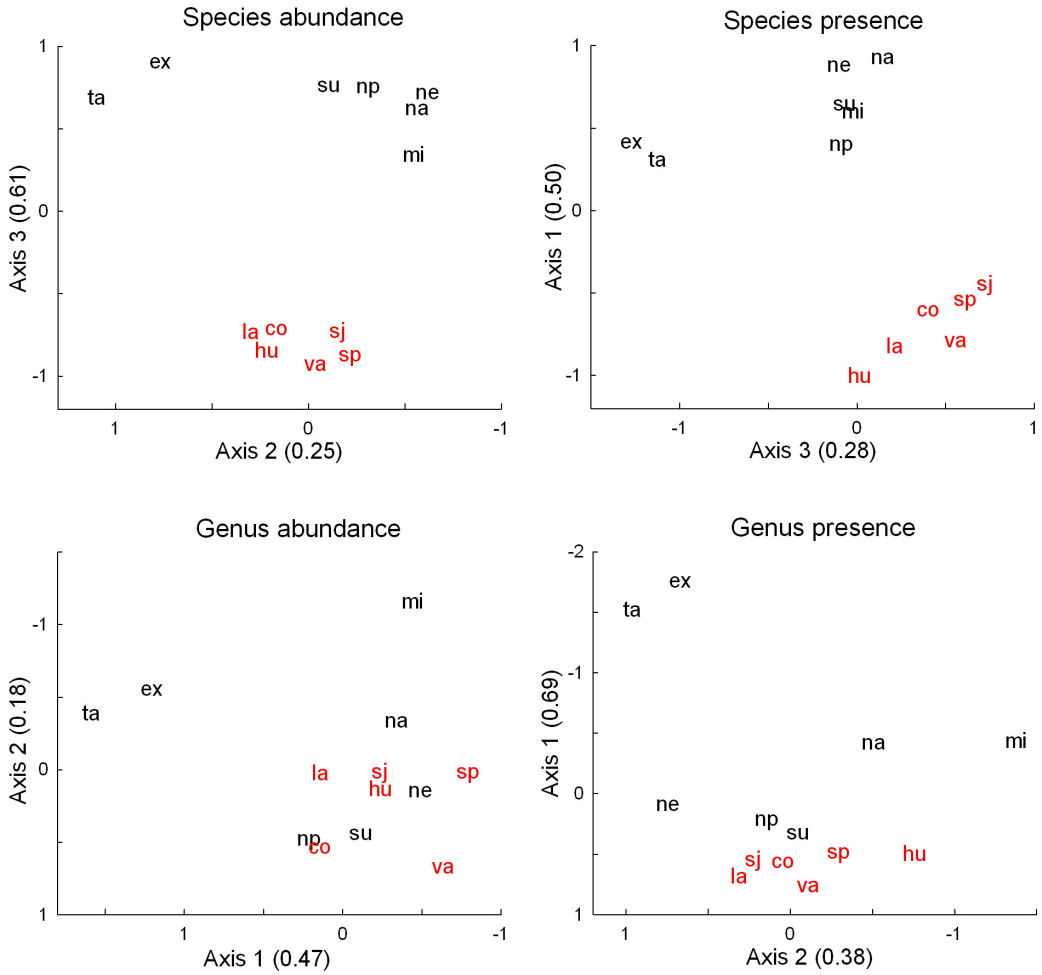


Figure 6.3. Nonmetric Multidimensional Scaling (NMS) ordination of 13 survey sites by bird species and genus composition. Sites are represented with their two-letter code, those north of the Amazon River are black, and those south of the river are red. Axes are those two NMS axes explaining the most variability in the original data; the r-squared values for correlation between the axes and the original data are shown in parentheses. NMS axis signs are arbitrary, and axes are oriented to show similarities among the graphs. Tarapoto (ta) and Expetroleros (ex) are the two sites that showed the highest degree of forest fragmentation in landscapes around the survey transects (see next chapter); while the distinctiveness of sites on opposite sides of the river clearly diminished at the genus level, the forest fragmentation effect did not.

Table 6.1. Site names and geographic descriptions, and bird survey dates. N and S indicate north and south of the Amazon River. Bird community composition differences were not associated with differences in survey date, year, or season.

Site	Code	Region	Coordinates	Dates surveyed
Expetroleros	ex	N	4° 4' S, 73° 27' W	26 Aug - 5 Sep 2005
Mishana	mi	N	3° 53' S, 73° 28' W	15-23 Sep 2005
Nauta	na	N	4° 26' S, 73° 34' W	3-11 Oct 2005
Tarapoto	ta	N	3° 46' S, 73° 26' W	29 Jul - 5 Aug 2006
Sucusari	su	N	3° 15' S, 72° 54' W	24 Sep - 3 Oct 2006
Nueva Esperanza	ne	N	3° 20' S, 72° 0' W	21-30 Oct 2006
Nuevo Peru	np	N	3° 16' S, 72° 0' W	3-12 Nov 2006
San Pedro	sp	S	4° 21' S, 73° 10' W	28 Oct - 5 Nov 2005
Siete de Julio	sj	S	4° 22' S, 73° 6' W	14-22 Nov 2005
Nuevo Valentin	va	S	4° 9' S, 73° 7' W	23 - 31 Aug 2006
Libertad Agraria	la	S	4° 9' S, 73° 5' W	1-8 Sep 2006
Huanta	hu	S	3° 29' S, 72° 2' W	27 Nov - 4 Dec 2006
Constancia	co	S	4° 7' S, 72° 55' W	2-9 Aug 2007

Survey sites within regions north or south of the Amazon River were not geographically nearer one another than were sites between regions (Table 6.2). I also evaluated associations between local environmental variables and regions, because observed differences in avian community composition between regions north and south of the Amazon may have been due to local environmental differences between the two regions. In addition, I examined associations between environmental variables and the range maps variable, and geographic distance. The two regionally defined site groups were not significantly different in soil characteristics, elevation or topographic variability (hilliness), surrounding landscape forest fragmentation measures, local forest basal area, stand densities, or plant species composition—despite considerable variability within regions in most of those variables (Table 6.2). Nearly the same results were obtained using the range maps variable in place of regions, although that variable was very weakly and inexplicably correlated with soil pH and the amount of forest edge within 4 km of survey transects.

Site elevations were typical of the western Amazon basin east of the Andean foreland and were somewhat uniform among plots, with site averages ranging between 100 and 140 m above sea level. Elevation was strongly correlated with distance among sites (Table 6.2), almost entirely because the four sites that were to the northeast of Iquitos and somewhat geographically separated from the remaining sites (su, ne, np, and hu) were lower in average elevation than the others. Those sites were downstream along the Amazon River from the other sites, so it is not surprising that their elevations were lower, but again, the degree of variation in average elevations was minor. Interestingly,

Table 6.2. Mantel correlations (R-values) among regional, species distributional (range map), and local environmental variables at 13 survey sites. Regions were north and south of the Amazon River; basal area only included stems <10 cm DBH; elevation statistics were calculated at the 2 km buffer radius; forest area, edge length, and edge per unit area were calculated at the 2 km and 4 km buffer radii. There were not important differences in the environmental variables measured between regions as defined by the Amazon River or by bird distributions. Neither were environmental variations correlated with geographic distance, except that the easternmost four sites were lower in average elevation and had lower densities of large trees. * P<0.05; ** P<0.01; *** P<0.001.

	Ln distance	Regions	Range maps
Regions	0.2	1.0	
Range maps	0.4**	0.95***	1.0
Elevation	0.51***	0.07	0.12
Elevation variance	-0.01	-0.09	-0.08
Soil pH	-0.17	-0.05	-0.11
Soil Ca+K+Mg+Na	-0.09	-0.06	-0.08
Soil loss on ignition	0.07	-0.07	-0.04
Soil clay+silt	0.08	0.06	0.05
Melastome species	-0.11	0.05	0.02
Pteridophyte species	-0.13	-0.01	-0.04
Basal area small stems	0.11	-0.08	0.03
Basal area large stems	-0.07	-0.08	-0.09
Tree density small stems	-0.04	-0.10	-0.09
Tree density large stems	0.49**	-0.06	0.07
Forest percent area 2 km	-0.09	-0.07	-0.04
Edge length 2 km	-0.09	-0.03	-0.01
Edge/area 2 km	-0.08	-0.04	-0.01
Forest percent area 4 km	-0.08	-0.05	-0.03
Edge length 4 km	-0.03	0.09	0.15*
Edge/area 4 km	-0.05	0.03	0.09

those same four sites also showed significantly lower large tree densities than the others, almost entirely accounting for a significant correlation between stand density and geographic distance (Table 6.2).

There was no relationship between bird species composition and year of survey ($r = 0.05$, $p = 0.29$ for abundance data; $r = -0.05$, $p = 0.37$ for presence data) or Julian day of year, using the fourth survey day at each site ($r = 0.02$, $p = 0.34$ for abundance data; $r = 0.07$, $p = 0.23$ for presence data). A direct comparison of community composition across years at the same site was possible only for the San Pedro site, for which additional data existed from a preliminary 2004 survey, using methods identical to those used in later years. Species compositional difference between years at San Pedro was lower (0.28 Steinhaus distance; 0.17 Sørenson distance) than for any other possible site-site comparison. Though this did suggest some annual variability, it probably also reflects the species identification learning curve of the surveyor, since 2004 was a preliminary year dedicated mainly to improving species identification knowledge. This result therefore tentatively suggests that annual variability and surveyor experience were, in combination, a less important source of variability among sites than were the biogeographic factors of interest. Surveyor experience was an even less important factor in subsequent years.

Geographic distance

There was no association between variation in raw geographic distance between sites and bird community compositional distance, in terms of species, genus, or family turnover (Table 6.3). There was a weakly significant association between the natural logarithm of

Table 6.3. Mantel correlations between bird community composition and geographic distance, regions, and species distributions among 13 bird survey sites. Each comparison was made using relative abundance and presence information. Comparisons were also made at the species, genus, and family taxonomic levels, considering all species. An additional comparison included only wide-ranging (WR) species, i.e., those 258 species whose range maps included all 13 sites. No tests were conducted for distributions (range maps) at the genus or family level. Partial Mantels are indicated by two variables separated by a minus sign, where the test is between the community composition data and the first variable, controlling for the second variable.

	Abundance (Steinhaus index)				Presence (Sørenson index)			
	Species	WR spp.	Genera	Families	Species	WR spp.	Genera	Families
Distance (km)	0.14	0.08	0.09	-0.01	0.08	0.04	0.00	-0.13
ln distance	0.27*	0.17	0.19	0.10	0.21	0.11	0.10	-0.15
Region	0.75**	0.38**	0.33**	0.25**	0.76***	0.28**	0.23**	0.01
Region - ln distance	0.73**	0.36**	0.31**	0.24**	0.74***	0.27**	0.21*	0.05
Range maps	0.81***	0.47***	~	~	0.81***	0.39***	~	~
Range maps - ln distance	0.79***	0.44***	~	~	0.81***	0.38**	~	~
Range maps - region	0.48**	0.38**	~	~	0.45*	0.41**	~	~

geographic distance and species composition using abundance data, but the relationship was not significant when only presence data were used, or when taxonomic levels above species were considered (Table 6.3, Figures 6.4 and 6.5). When geographic distances were weighted to account for the presence of the Amazon River as a dispersal barrier, the correlation between species composition and dispersal distance did not surpass that between species composition and the Amazon River as a simple regional boundary, but rather approached it asymptotically as the weighting coefficient increased in value (Fig. 6.6).

Species distributional limits

Species composition expected on the basis of range maps was highly correlated with observed species composition (r^2 = .62, abundance data), more so than any other variable, and it remained so when geographic distance was partialled out (Table 6.3, Figure 6.4). When only wide-ranging species were considered, the correlations remained very high. R-values were similar for abundance data and presence data when all species were included, but when range-restricted species were removed, r-values were higher for abundance data than for presence data, as expected.

Biogeographic regions

The regional distinction, whereby sites were situated either north or south of the Amazon River, was very highly correlated with bird species and genus compositions, and it remained highly significant when geographic distance was partialled out (Table 6.3,

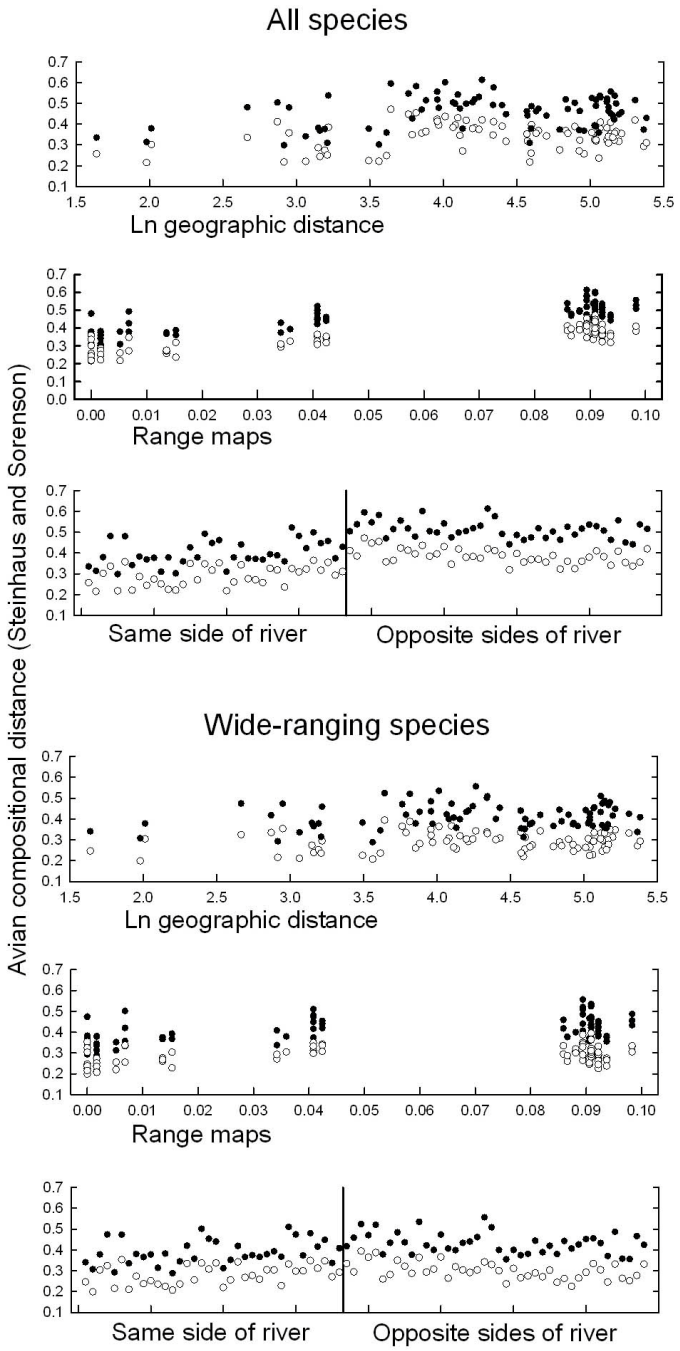


Figure 6.4. Steinhaus (black dots) and Sørenson (white dots) community compositional difference between all 78 possible site pairs. Indices were calculated including all bird species, and including only species whose ranges included all sites (wide-ranging species). The x-axis shows difference between site pairs in the variable indicated; in the case of the binary river variable (same side or opposite sides), site pairs within the two groups are ordered by increasing geographic distance.

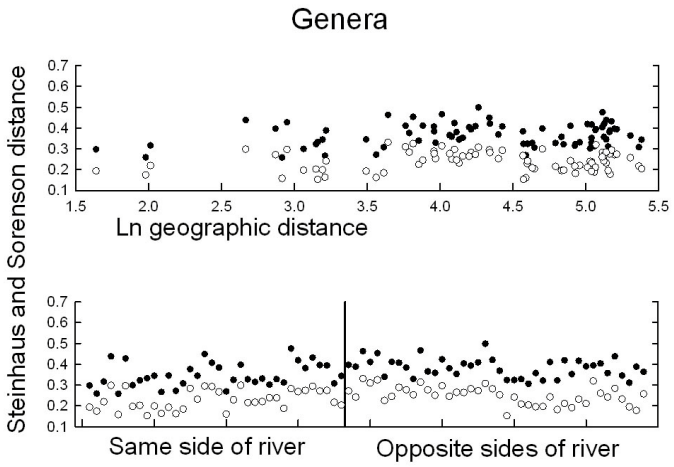


Figure 6.5. Steinhaus (black dots) and Sørenson (white dots) community compositional difference between all 78 possible site pairs. Indices were calculated at the genus level, including all species. The x-axis shows difference between site pairs in the variable indicated; in the case of the binary river variable (same side or opposite sides), site pairs within the two groups are ordered by increasing geographic distance.

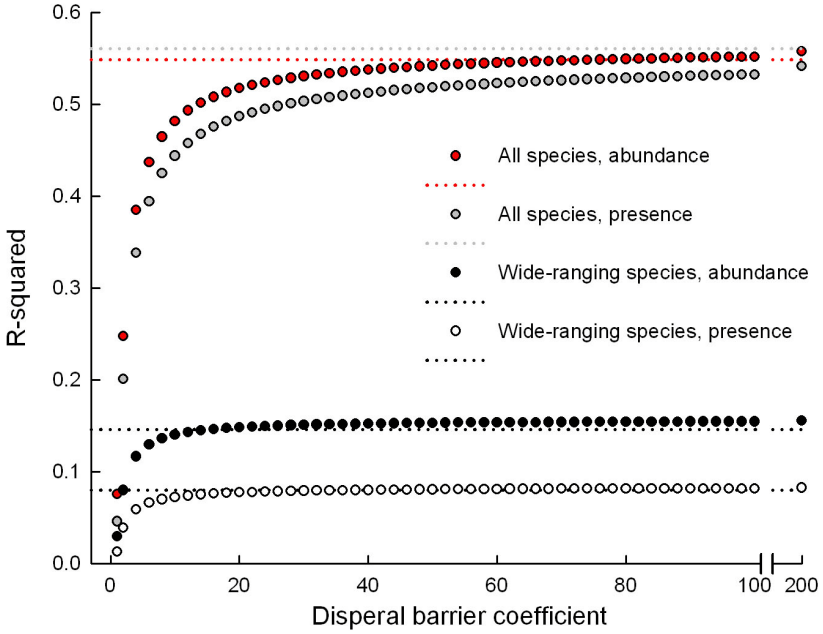


Figure 6.6. Correlations between dispersal distance and variation in species composition among sites. The weight given to dispersal across the Amazon River increased as the value of the dispersal barrier coefficient increased, while dispersal distance among sites on the same side of the river was unaffected. Dotted lines represent the r-values for correlation between the respective dataset and the simple regional distinction between sites north and south of the Amazon River. Weighted dispersal distance r-values approached the simple regional values asymptotically, suggesting that river-based dispersal weights only increased explanatory power because they increasingly resembled the simple regional distinction as the value of the weighting coefficient dominated the geographic distance value. Thus, weighted or un-weighted dispersal distance could not explain variation in species composition among sites better than the distance-independent regional distinction.

Figures 6.4 and 6.5). More than half of the variability in species composition ($r^2 = .53$, abundance data) could be accounted for with this binary variable, which was also very highly correlated with the rangemaps variable ($r = 0.95$, $p = 0.001$). The smallest differences in species composition between any two sites on opposite sides of the river were 44 percent Steinhaus difference and 32 percent Sørenson difference, whereas the smallest differences overall were 30 percent and 21 percent, respectively.

Indicator species analysis identified 55 species with a significant ($p < 0.05$) indicator value for regions north and south of the Amazon River (Tables 6.4a and 6.4b, Figure 6.7). This represented 16 percent of all species in the dataset, and 25 percent of the 214 species included in indicator species analyses. Twenty of those 55 species were more abundant north of the river, and 35 were more abundant south of the river. Only 26 of those species were completely restricted to plots on one side of the Amazon; a great deal of the regional difference in community composition was caused by those 29 species that showed systematic differences in abundance, rather than presence, across the river. While those species with distributional limits at the Amazon River are largely known, wide-ranging species with systematic differences in abundance across the river have rarely been described.

The same indicator species analysis identified 77 species with significantly different abundances between the two regions at the $p < 0.10$ level. Twenty-six species were more abundant north of the river, and 51 were more abundant south of the river. None of the additional 22 species (Table 6.4c) was completely restricted to either region.

Table 6.4a. Results of Indicator Species Analysis for regions north and south of the Amazon River. Species limit = species with distributional limits at the Amazon, as described in Schulenberg et al. (2006); Subspecies limit = species whose distributions extend to both banks of the Amazon, but that comprise described subspecies which replace one another on opposite sides of the river in the Iquitos region (see text for references); Region = the region in which the species was detected more frequently (exclusively, in many cases) and consistently across sites within that region; IV = Indicator value. Some species with regional distributional limits had relatively low indicator values because they were not consistently detected within their range.

Species	Species limit	Subspecies limit	Region	IV	P
Odontophorus stellatus	x		S	66.7	<0.05
Pyrrhura picta	x		S	100	<0.01
Pyrrhura melanura	x		N	85.7	<0.01
Pionites melanocephalus	x		N	100	<0.01
Pionites leucogaster	x		S	100	<0.01
Phaethornis philippii	x		S	97.5	<0.01
Phaethornis bourcierii	x		N	100	<0.01
Galbula albirostris	x		N	71.4	<0.05
Galbula cyanicollis	x		S	100	<0.01
Pteroglossus pluricinctus	x		N	100	<0.01
Pteroglossus beauharnaesii	x		S	83.3	<0.01
Thamnophilus aethiops	x		S	83.3	<0.01
Megastictus margaritatus	x		N	71.4	<0.05
Thamnomanes ardesiacus	x		N	100	<0.01
Thamnomanes saturninus	x		S	100	<0.01
Thamnomanes caesius	x		N	100	<0.01
Myrmotherula sclateri	x		S	100	<0.01
Myrmeciza hemimelaena	x		S	100	<0.01
Gymnopithys leucaspis	x		N	85.7	<0.05
Gymnopithys salvini	x		S	100	<0.01
Phoenicircus nigricollis	x		N	97.6	<0.01
Pipra erythrocephala	x		N	100	<0.01
Pipra rubrocapilla	x		S	100	<0.01
Thryothorus coraya	x		N	85.7	<0.05
Thryothorus genibarbis	x		S	66.7	<0.05
Tachyphonus cristatus	x		N	97.9	<0.01
Tachyphonus rufiventer	x		S	83.3	<0.05
Lanio versicolor	x		S	100	<0.01

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Table 6.4b.

Species	Species limit	Subspecies limit	Region	IV	P
Capito auratus		x	N	61.6	<0.01
Xiphorhynchus ocellatus		x	N	88.1	<0.01
Xiphorhynchus elegans		x	S	100	<0.01
Epinecrophylla haematonota		x	S	81.6	<0.05
Myrmotherula hauxwelli		x	N	80.5	<0.05
Cercomacra cinerascens		x	S	73.7	<0.05
Cercomacra serva		x	S	79.2	<0.01
Myrmoborus myotherinus		x	S	64.9	<0.05
Lophotriccus vitiosus		x	S	67.2	<0.01
Microcerculus marginatus		x	N	75.8	<0.05
Ramphocaenus melanurus		x	S	92.8	<0.01
Tachyphonus surinamus		x	S	77.3	<0.05
Ibycter americanus			S	71.7	<0.05
Amazona farinosa			S	77.5	<0.05
Galbula dea			S	74.8	<0.05
Celeus elegans			N	79.8	<0.05
Philydor pyrrhodes			S	73.1	<0.05
Dendrocincla fuliginosa			N	77.4	<0.05
Myrmotherula brachyura			S	90.6	<0.01
Myrmotherula axillaris			S	61.7	<0.05
Hylophylax naevius			S	75.2	<0.01
Hemitriccus minimus			S	74.5	<0.05
Legatus leucophaius			S	79.9	<0.05
Attila citriniventris			S	78.5	<0.05
Tangara callophrys			N	85.7	<0.05
Cyanocompsa cyanoides			S	67.7	<0.05
Euphonia xanthogaster			S	79.2	<0.05
Euphonia rufiventris			S	61.8	<0.01

Continued on next page.

Table 6.4c. Species with significant associations at $0.05 < P < 0.10$.

Species	Species limit	Subspecies limit	Region	IV	P
Heliodoxa schreibersii	x		N	59.8	<0.10
Malacoptila fusca	x		N	57.1	<0.10
Lanio fulvus	x		N	57.1	<0.10
Eubucco richardsoni		x	N	54.9	<0.10
Synallaxis rutilans		x	N	57.1	<0.10
Deconychura longicauda		x	S	65.7	<0.10
Dendrocolaptes certhia		x	N	66.1	<0.10
Phlegopsis erythroptera		x	S	59.4	<0.10
Dixiphia pipra		x	S	68.7	<0.10
Tinamus major			S	70	<0.10
Tinamus guttatus			S	70	<0.10
Crypturellus cinereus			S	72.8	<0.10
Pharomachrus pavoninus			S	69.1	<0.10
Jacamerops aureus			N	63.5	<0.10
Sclerurus mexicanus			S	51.9	<0.10
Thamnophilus murinus			S	56.6	<0.10
Myrmeciza fortis			S	63.1	<0.10
Tyrannulus elatus			S	67.6	<0.10
Conopias parvus			S	68.6	<0.10
Vireolanius leucotis			S	59.8	<0.10
Dacnis cayana			S	66.6	<0.10
Psarocolius bifasciatus			S	64.8	<0.10

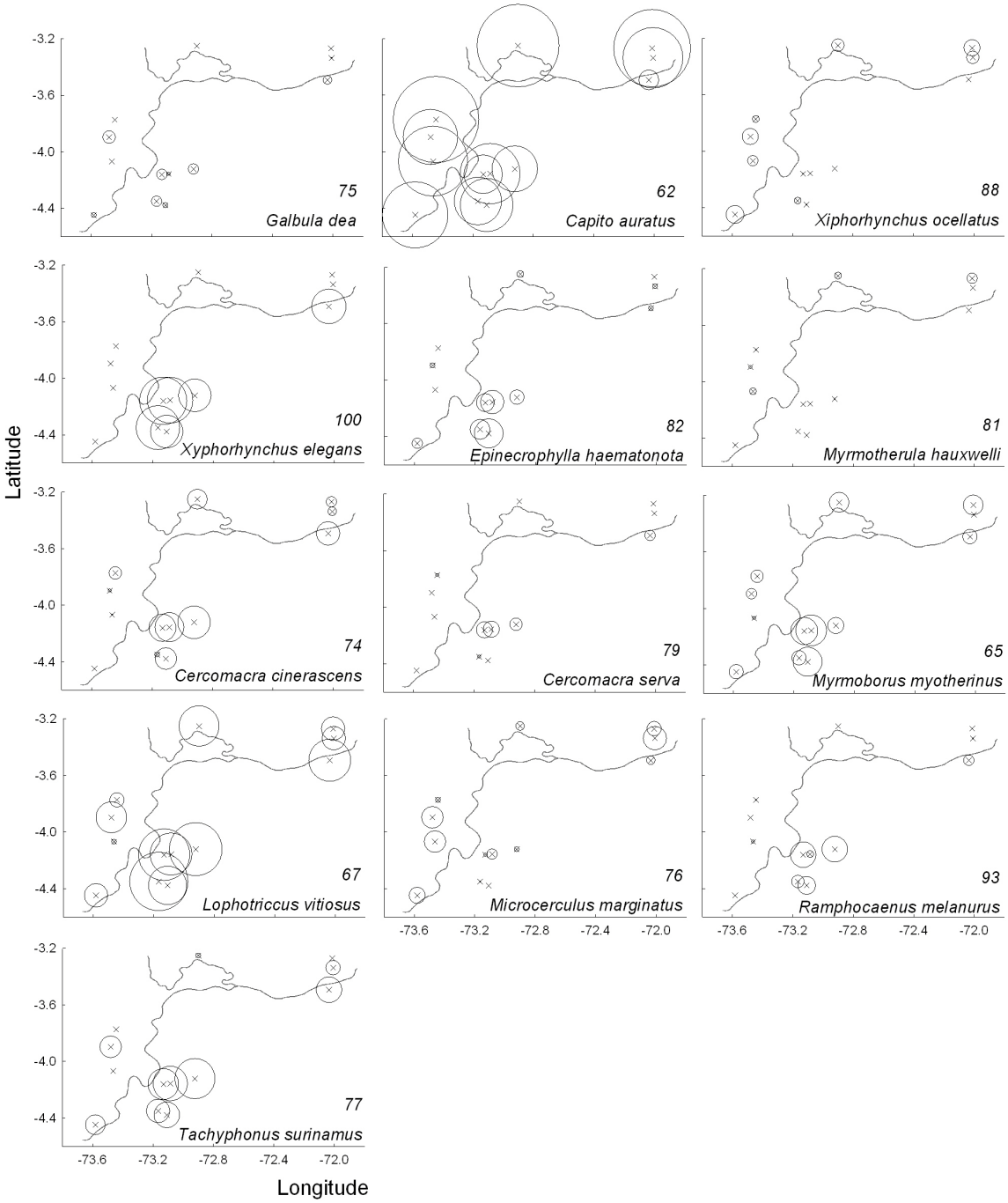

Figure 6.7a. Relative abundances of species with significant ($p < 0.05$) indicator values for regions north or south of the Amazon River. Circles are proportional to the number of detections on each plot. Indicator value, shown above the species name, ranges from 0 to 100, where 100 represents perfect fidelity to one group and representation at every plot in that group. Species shown here are those that range on both sides of the Amazon, but that are comprised of separate subspecies north and south of the Amazon.

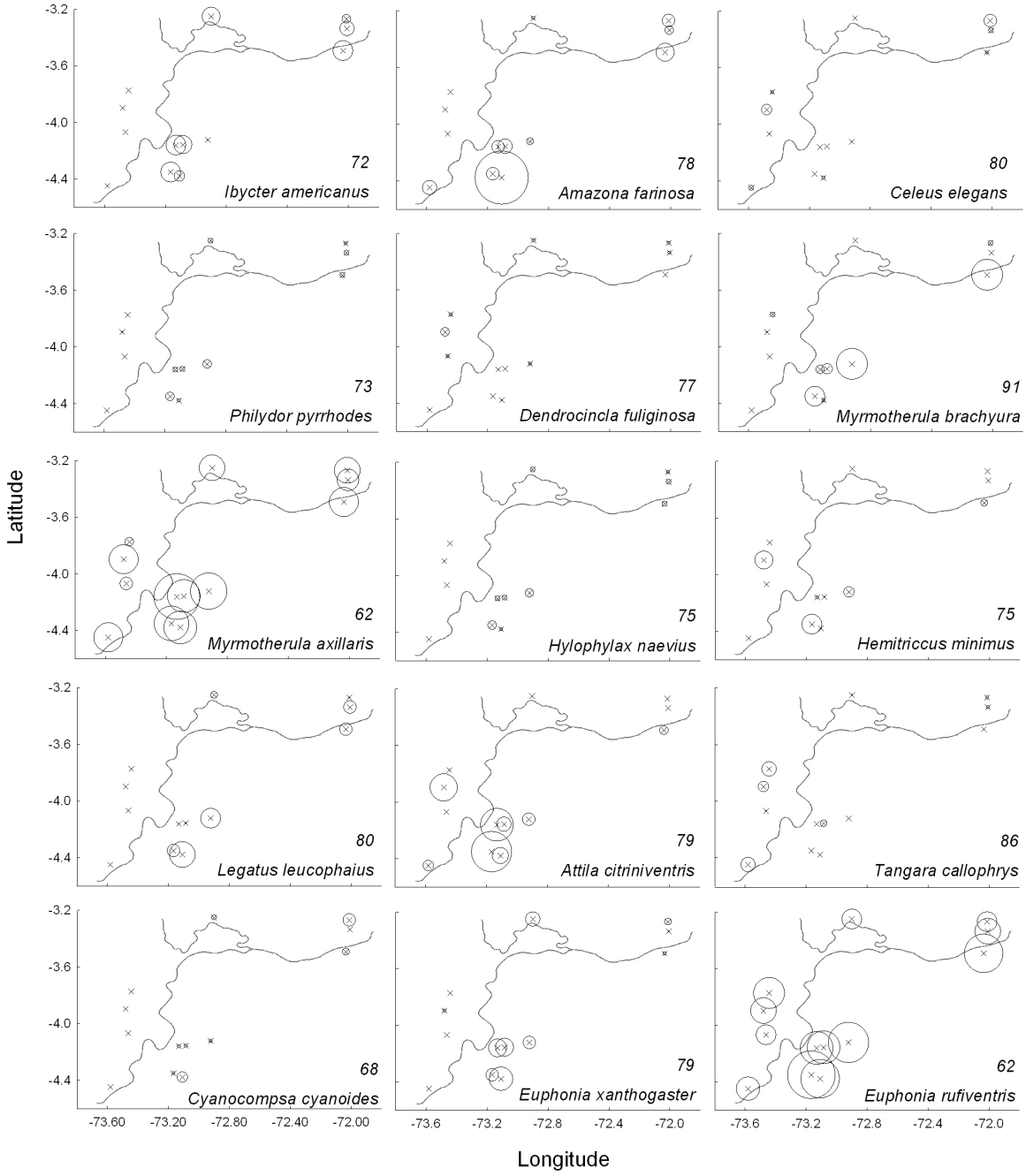

Figure 6.7b. Species shown here are all those with a significant ($p < 0.05$) indicator value, that range on both sides of the Amazon, and that are comprised of only a single subspecies that ranges north and south of the Amazon.

When species were grouped by canopy stratum occupancy, terrestrial and understory species showed slightly more regional difference than did canopy species, with midstory species appearing intermediate. The species showing a significant regional association in indicator species analysis were not mainly terrestrial or understory species. However, within that group of species, those with distributional limits at the Amazon tended to be understory species, whereas those occurring in both regions but with regional abundance differences tended to be canopy species. Thus, there appeared to be some relationship between distributional limitation and lower-stratum habitat occupancy.

Subspecies limits

Species that occurred in both regions but that showed regional abundance differences tended to be species with described parapatric subspecies replacements on opposite sides of the Amazon in the Iquitos region. There were 279 species in the dataset known to occur in both regions (inter-regional species), of which 183 occurred at a sufficient number of sites (more than three) for tests of single-species abundance differences between regions with indicator species analysis. Thirty-nine (21 percent) of those species had subspecies replacements across the Amazon (18 percent of all 279 species considered had subspecies replacements). Twenty-eight species ranged in both regions and showed regional abundance differences at the $p < 0.05$ level, and of those, 12 (43 percent) had subspecies replacements across the Amazon. Among inter-regional species that showed no regional abundance difference, only 17 percent had subspecies replacements. Forty-

seven inter-regional species had significant regional abundance differences at the $p < 0.10$ level, and 18 (38 percent) of those had regional subspecies replacements. At the $p < 0.10$ level, only 15 percent of wide-ranging species with no regional abundance difference had subspecies replacements. Thus, wide-ranging species with regional abundance differences had regional subspecies replacements at roughly twice the frequency expected by chance ($\chi^2 = 7.78$, $p = 0.005$, and $\chi^2 = 8.10$, $p = 0.004$, for species with abundance differences at $p < 0.05$ and $p < 0.10$, respectively. See also Table 6.4.).

DISCUSSION

Geographic distance and dispersal limitation

The weak relationship that did exist between species relative abundance and geographic distance was correlated with the division between the north and south banks of the Amazon River, and it is likely that the regional boundary, rather than distance per se, was responsible for the observed distance effect. This effect might be termed dispersal limitation, since those species are limited at the Amazon River, but it is not at all clear that they are limited by endogenous dispersal abilities, rather than by exogenous factors such as social interactions with competitor species on the opposite bank.

No 'optimal' weighting value was found for a dispersal limitation coefficient for the Amazon River, beyond which higher values result in lower correlation coefficients. Since the highest weighting values were those that most completely erased the influence

of geographic distance and replaced it with the distance-independent riverine boundary, these results support the general finding that the riverine boundary appears to influence avian community composition via some process other than distance-mediated dispersal limitation.

Distributional limits

There was a very strong association between variation in species composition and distributional limits, which was in turn highly correlated with the regional division. It was a slightly stronger association than that between species composition and regions, and it was stronger than would be expected from the contribution of only those 52 species that are represented in range maps as having distributional limits at the Amazon River in the Iquitos region.

When only presence data were considered, mean among-sites species turnover was about 35% (Fig. 6.1), and about 62% of this variability was associated with species turnover as estimated from range maps (r^2 = 0.62, Table 6.3). As a very coarse estimation, about 22% of total among-sites pattern in species presence was therefore associated with distributional limits (0.35 × 0.62 = 0.217); an additional 65% being simply among-sites homogeneity. The 52 species with distributional limits at the Amazon River represent 16% of the 334 species included in the survey samples. There were an additional 24 species with distributional limits in the study region that did not correspond to the Amazon River, so that a total of 23% of species in the dataset had distributional limits in the study area. This agrees well with the 22% of overall pattern in species

presence, derived from the survey data, which was associated through Mantel tests with variation in species composition according to range maps.

When using relative abundance data, however, the mean among-sites species composition difference was much higher (47%; Fig. 6.1), while the correlation between species composition and range maps was no different than when presence data were used ($r^2 = 0.62$, Table 6.3). About 29% of the terra firme bird community therefore showed abundance variability that was associated with distributional limits ($0.47 \times 0.62 = 0.291$). Thus, the range maps of the 76 species (23% of total) with described distributional limits in the region were correlated with more variability in species composition than they can possibly account for in strict terms of presence-absence of those 76 species. This discrepancy was apparently created by those 47 species that range widely on both sides of the Amazon River, but whose relative abundances varied systematically between the two regions (Table 6.4, Fig. 6.5). Additional species may have shown variations in abundance that correlated with other range map limits in the study region besides those aligned with the Amazon River.

It should be borne in mind that species distributions are not taken as a fundamental explanatory factor for community composition, but rather as a practical one. I only examined one proximal cause of distributional limits, namely, the Amazon River, and even in this case, the ultimate evolutionary and ecological causes are controversial. This is discussed in the following section.

Even while the ecological and evolutionary factors influencing present-day species distributions are not fully known, good range maps can nonetheless be used to

effectively predict important components of local community composition. This may be true to a greater extent than has typically been recognized for Amazonian regions, for which emphasis has typically been placed on the comparatively wide distributions of taxa.

While there are in fact many widely distributed species, this may be countered by the extraordinary taxonomic diversity of the Amazon basin—for every widely distributed species, there is another relatively endemic species, and important distributional limits are likely to be found almost anywhere in the western Amazon. In addition, highly endemic species are, almost by definition, less well accounted for in regions such as the Amazon basin, where biologists' access to sites away from rivers is very limited. Many of the recently described avian taxa in the western Amazon are restricted to special terra firme habitats, and are probably quite limited in overall distribution (Whitney and Alvarez 1998, Krabbe et al. 1999, O'Neill et al. 2000, Alvarez and Whitney 2001, Isler et al. 2001, Isler et al. 2002, Whitney et al. 2004, Whitney and Alvarez 2005, Lane et al. 2007). Another category of newly designated species are those that were until recently regarded as subspecies of a widely distributed species, but are now considered to be several parapatric species, each of whose distribution is only a fraction of the superspecies distribution (Isler et al. 1999, Krabbe et al. 1999, Whitney et al. 2000, Isler et al. 2002, Isler et al. 2007a, Isler et al. 2007b). In both of these cases, two general effects are an increase in known gamma diversity and a concomitant strengthening of the correlation between known distributional limits and beta diversity. As improvements of this kind are made in the basic biogeographic descriptions of Amazonian taxa, their

utility for understanding community diversity at relatively fine spatial scales is likely to become more highly appreciated.

Regional limits

Species-level distributional limits were the primary factor constituting avifaunal biogeographic difference between regions, a notion reinforced by the finding that the simple distinction between sites north and south of the Amazon River has less explanatory power than do species range limits per se. Those two variables were themselves very highly correlated, and most of the variability explained by the regional distinction is apparently due to species distributional limits at the Amazon. The difference between regions was not, however, strictly a result of those species-level limits. Systematic differences in the abundances of species that range across both regions also contributed strongly to the regional difference.

The correlation between community composition and region was stronger, for example, when species abundance data were included than when only presence was considered. Those wide-ranging species whose abundances varied between regions were clearly identified in indicator species analysis (Table 6.4, Fig. 6.7). In addition, a strong difference in community composition remained between regions when all species currently described as having range limits at the Amazon River were removed from the analysis. Because occurrence records from both sides of the river have historically tended to be required for the river not to be viewed as a range limit for any given species, it is

very unlikely that species with real limits at the river were mistakenly included in that analysis. Nonetheless, there were some wide-ranging species included that, while present at several sites on one side of the river, were absent from all sites on the opposite side. These were all species that are known to occur on both banks in nearby areas. They likely represent the extreme cases of species whose abundances vary systematically between regions, and so they were rare enough on one side to escape detection in my sample. In at least some, and possibly all, cases they represent species whose habitat associations differ between regions. *Xiphorhynchus elegans*, for example, was absent from all sites north of the river because it specializes to some degree on várzea forest in that region, whereas it is common in terra firme south of the river, and so was present on those study sites. It should be noted that these two populations are separate subspecies, and that subspecific differences between regions may explain abundance differences precisely because of ecological differences between closely related taxa, as discussed below.

The striking difference in avian community composition between the two regions examined here raises the question of why these differences exist, and in particular, whether they might be driven by environmental differences between the regions. This appears unlikely, as there were no systematic differences between regions in any of the environmental variables I measured. Variability in topography, soils, local deforestation, forest structure, and floristic composition was greater among sites within either region than between regions. Worded another way, the apparent lack of strong environmental differences between the two regions raises the question of how such strong differences in bird community composition could have arisen.

A more compelling reason for within-species differences in abundance on opposite sides of the Amazon may be that at least some of the taxa themselves differ ecologically between the two regions. Many of the species in the dataset that consisted of subspecies described in the literature as allopatric on opposite sides of the river were found to have different abundances between the two regions. Conversely, roughly 40 percent of all species that showed a regional abundance effect had described subspecies disjunctions at the Amazon River in the study area. Many of these subspecies are recognizable visually or by voice, whereas ecological or behavioral differences have not been as well described, except in the most obvious cases. The case of *Xiphorhynchus elegans*, mentioned above, is a good example. This species' local habitat preferences are different on opposite sides of the river, and the difference is easily observable because várzea and terra firme habitats are easily distinguished by people. A more subtle difference in habitat associations, leading to differing abundances in similar habitats, could easily exist for many other subspecies pairs, and could account for the regional abundance differences that I found for many of them.

It is important to note that the idea of ecological difference between closely related, parapatric taxa is somewhat at odds with the idea that parapatric species remain parapatric precisely because they are not ecologically different, and they therefore competitively exclude one another from their respective ranges. The latter notion may be seen as a product of the stress that has been historically placed on the role of competition in community ecology, and in fact I discuss competition in this dissertation as a possible enforcing mechanism, in part, for the strong river effect that I observed. It should be

borne in mind that there is no reason these apparently opposing effects may not be operative for different taxa in the same communities, that competitive exclusion may not in fact require absolute ecological similarity, and most importantly, that both of these explanations are only offered tentatively here as hypotheses for additional research. On the other hand, if dispersal across the river is actually physically prevented by the river floodplain for at least some subspecies, then the question of competitive exclusion is moot.

In summary, historically evolved genetic differences between subspecific taxa may be one of the principle drivers of the regional effect that was observed even when river-bounded species were removed from the analysis. Of course, the regional effect caused by those river-bounded species is also likely a historical effect. The regional effect in its entirety therefore appeared to be largely an effect of evolutionary and biogeographic history, expressed strongly at the species and subspecies levels and more weakly at the genus level, rather than an effect of present-day environmental differences between forests in the two regions. The present-day mechanism preventing dispersal across the river floodplain remains obscure for most, if not all, species, and may be different for different species.

Chapter Seven

Bird Communities and Local Environments

RESULTS

Soils and topography

Variation in bird species composition was not significantly correlated with variation in any soil variable, when all species were included and when either abundance or presence data were used (Table 7.1). When only wide-ranging species were included, there were significant correlations with Ca, Mg, and Na concentrations, and with summed cation concentration, but only when bird abundance data were used. Bird genus composition was correlated with Ca concentrations and with summed cation concentration. Neither fine particle (clay and silt) proportions nor loss on ignition were correlated with any measure of bird community composition.

Average elevations were quite similar among survey sites, and typical of the western Amazon basin east of the Andean foreland. Within-site elevation ranges, while fairly narrow, in most cases exceeded variation among sites. Variation in bird species and genus composition were not correlated with variation in elevation range or variance at any buffer radius around survey sites (Table 7.2).

Table 7.1. Mantel correlations (R-values) between bird community composition and soil variables at 13 survey sites in the Peruvian Amazon. Each comparison was made using relative abundance information as well as presence information, at the species and genus taxonomic levels. The wide-ranging species category (WR) includes only those 258 species whose known distributions covered all 13 survey sites. * $0.03<P<0.05$.

	Abundance			Presence		
Soil variable (ln)	All spp.	WR spp.	Genera	All spp.	WR spp.	Genera
pH	-0.19	-0.23	-0.18	-0.14	-0.18	-0.16
Al	-0.18	-0.26	-0.28	-0.16	-0.29	-0.28
Ca	0.09	0.19*	0.18*	0.08	0.16	0.19
K	0.03	0.12	0.07	0.05	0.13	0.02
Mg	0.13	0.27*	0.24	0.08	0.19	0.18
Na	0.21	0.25*	0.19	0.17	0.15	0.08
Ca+K+Mg+Na	0.11	0.23*	0.20*	0.09	0.17	0.20*
Loss on Ignition	0.01	0.05	0.00	0.04	0.12	0.09
Clay, silt	0.10	0.15	0.09	0.13	0.17	0.15

Table 7.2. Mantel correlations (R-values) between bird community composition and within-site elevation range and variance, including landscapes within four increasingly wide radii around survey transects. Bird observations were grouped at the species and genus levels, using both abundance and presence data. The wide-ranging species category (WR) includes only those 258 species whose known distributions covered all 13 survey sites. There were no statistically significant correlations at the $P < 0.05$ level.

Elevation range vs. avian composition						
	Abundance			Presence		
Buffer radius	All spp.	WR spp.	Gen	All spp.	WR spp.	Gen
150 m	-0.13	-0.18	-0.15	0.01	0.02	0.07
500 m	-0.10	-0.18	-0.13	-0.01	-0.05	-0.06
1 km	-0.04	-0.11	-0.03	0.06	0.03	0.09
2 km	-0.04	-0.03	0.01	0.05	0.12	0.21
Elevation variance vs. bird composition						
150 m	-0.12	-0.14	-0.13	-0.02	0.02	0.05
500 m	-0.09	-0.09	-0.05	0.00	0.10	0.11
1 km	0.00	-0.02	0.03	0.12	0.22	0.25
2 km	-0.18	-0.19	-0.22	-0.13	-0.11	-0.07

Plant species composition

A total of 113 Pteridophyte and 111 Melastome species and morphospecies were recorded in 34 and 14 genera, respectively. Sites showed stronger differences in plant species composition than in bird species composition, sometimes reaching nearly complete distinctiveness in both Pteridophyte and Melastome species composition (Fig. 7.1). The sites were chosen in advance for their difference in plant species composition, so naturally they grouped into clear classes in NMS ordination, whether Pteridophyte or Melastome species composition was used (Fig. 7.2). Sites clustered into two classes, and the same site groupings resulted from ordination with either plant group, but the classes were more discreet for Pteridophytes than for Melastomes. The best NMS solution included two axes for Melastome composition. Two NMS axes are shown for Pteridophyte composition in Figure 7.2 for comparison to the other two ordinations. However, the two-axis solution for Pteridophytes did not reduce stress sufficiently to be considered more efficient than the one-axis solution.

Soil cation concentrations were strongly, positively correlated with the species composition of both plants groups, while Al concentration, pH, and LOI were not (Table 7.3). Fine particle concentration was correlated with Melastome composition, but not with Pteridophyte composition. Consistent with previous studies, Pteridophyte composition was slightly more highly associated with cation concentrations than was Melastome composition.

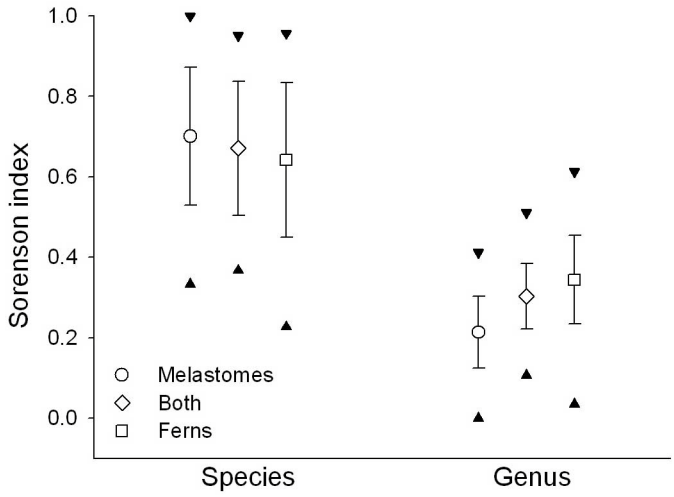

Figure 7.1. Mean (± standard deviation) plant community composition differences among survey site pairs (n = 78), For Melastomes, Pteridophytes (ferns), and both groups together. The Sørenson index uses species presence only, and is shown as a distance, on a scale of 0.0 (complete similarity) to 1.0 (complete difference). Triangles show minimum and maximum values. Community distinctiveness increased with increasing taxonomic resolution, more so for Melastomes than for Pteridophytes. Melastome genus composition may have been less divergent among sites than was Pteridophyte genus composition, probably due to the dominance within Melastomataceae of the widespread and speciose genus *Miconia*.

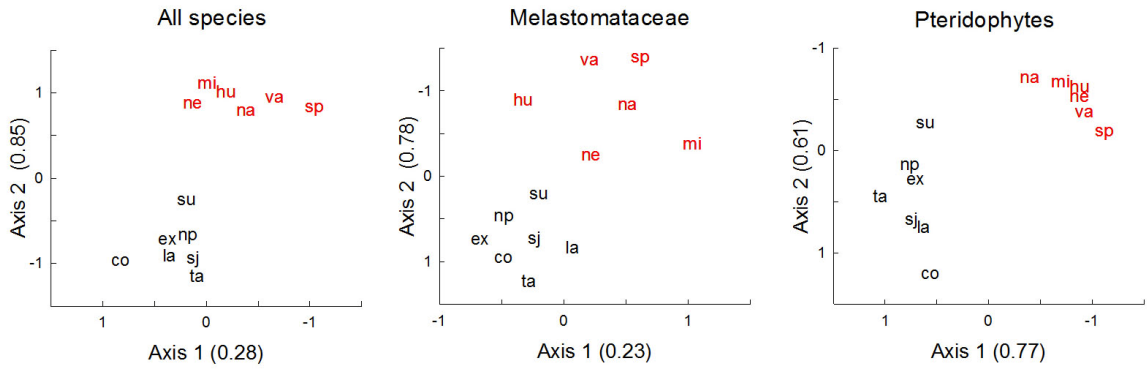

Figure 7.2. Nonmetric Multidimensional Scaling (NMS) ordination of 13 survey sites by plant species composition. Sites are represented with their two-letter code. Sites chosen in advance as those on nutrient-poor, sandy soils are shown in red, and those on nutrient-rich, clayey soils are shown in black. The leftmost graph shows both plant groups combined. Axes are those two NMS axes explaining the most variability in the original data; the r-squared values for correlation between the axes and the original data are shown in parentheses. NMS axis signs are arbitrary, and axes are oriented to show similarities among the graphs.

Table 7.3. Mantel correlations (R-values) between soil variables and plant species composition and richness across 13 survey sites in the Peruvian Amazon. Composition tests were performed with presence data (Sørenson index) at the plant species or morphospecies level. ** P<0.01; *** P<0.001.

	Composition (Sørenson)		Richness	
Soil variable	Pteridophytes	Melastomataceae	Pteridophytes	Melastomataceae
pH	0.11	-0.03	-0.13	-0.14
Al	-0.03	-0.15	-0.07	-0.17
Ca	0.75***	0.66***	0.09	-0.04
K	0.58***	0.60***	0.08	-0.04
Mg	0.82***	0.63**	0.07	-0.03
Na	0.53**	0.65***	0.15	-0.12
Ca+K+Mg+Na	0.78***	0.65**	0.07	-0.08
Loss on Ignition	-0.01	-0.03	-0.08	-0.15
Clay, silt	0.14	0.45**	0.05	-0.01

When all bird species were included, Melastome species composition was correlated with both bird species and genus composition, while fern composition was not correlated with bird composition at either taxonomic level (Table 7.4, Figure 7.3). Correlations with Melastomes were stronger at the bird genus level than at the species level, and stronger for abundance data than for presence data. When only wide-ranging species were included, the strength of correlations at the species level increased substantially, and fern species composition was significantly correlated with wide-ranging bird species composition (Table 7.4, Figure 7.4). Bird abundance data remained more strongly correlated than did presence data with either plant group. The full plant dataset, including all fern and Melastome species, was also significantly correlated with bird species composition, though not as strongly as were Melastomes alone.

Indicator species analysis resulted in 22 species, or nearly seven percent of all species in the dataset, with a significant ($p<0.05$) indicator value for sites with Melastome compositions reflecting either nutrient-rich conditions (13 species) or nutrient-poor conditions (9 species; Table 7.5; Fig. 7.5). There were 35 species with significant indicator values at the $p<0.10$ level, of which 22 were associated with nutrient-rich sites and 13 with nutrient-poor sites.

Table 7.4. Mantel correlations (R-values) between bird community composition and vegetation composition and structure variables at 13 survey sites in the Peruvian Amazon. Each comparison was made using relative abundance information as well as presence information; and at the species and genus taxonomic levels. The wide-ranging species category (WR) included only those 258 bird species in the survey dataset whose known distributions covered all 13 survey sites. * P<0.05; ** P<0.01.

	Abundance			Presence		
Forest floristics	All spp.	WR spp.	Genera	All spp.	WR spp.	Genera
Pteridophytes	0.14	0.22*	0.17	0.11	0.15	0.09
Melastomataceae	0.28*	0.37**	0.35**	0.26*	0.33*	0.28*
Pteridophytes + melastomes	0.22	0.31**	0.27**	0.20	0.25*	0.18
Forest structure						
Basal area <10 cm DBH	0.25*	0.40*	0.45**	0.21*	0.43**	0.46**
Basal area >10 cm DBH	-0.01	0.03	0.15	-0.05	0.02	0.16
Basal area small + large	-0.01	0.03	0.16	-0.05	0.02	0.17
Stand density <10 cm DBH	0.09	0.21	0.25	0.10	0.27*	0.26
Stand density >10 cm DBH	-0.09	-0.13	-0.09	-0.07	-0.04	-0.06
Stand density small + large	0.20	0.23	0.27	0.19	0.23	0.23
Leaf litter depth	-0.15	-0.16	-0.21	-0.08	-0.08	-0.22
Percent transect in gap phase	0.11	0.15	0.25	0.08	0.12	0.23

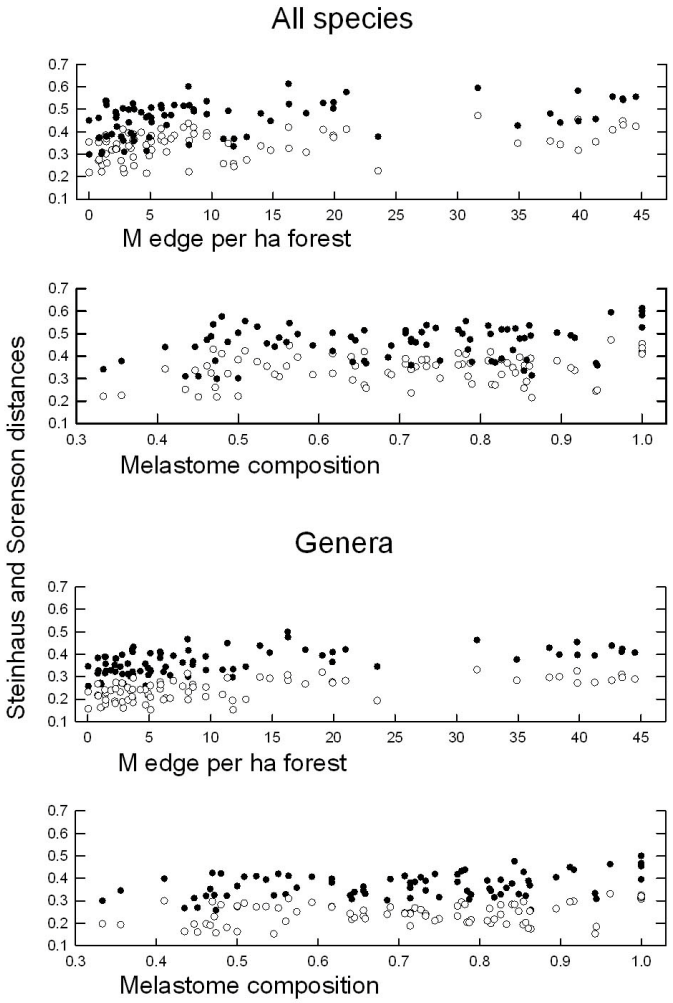

Figure 7.3. Steinhaus (black dots) and Sørenson (white dots) community compositional difference between all 78 possible site pairs. Indices were calculated including all bird species, at the species and genus levels. The x-axis shows difference between site pairs in the variable indicated; the Sørenson index was used to estimate Melastome compositional difference, and the forest edge-to-area ratio was measured within 4 km of survey sites. Associated Mantel correlations are given in Table 7.4.

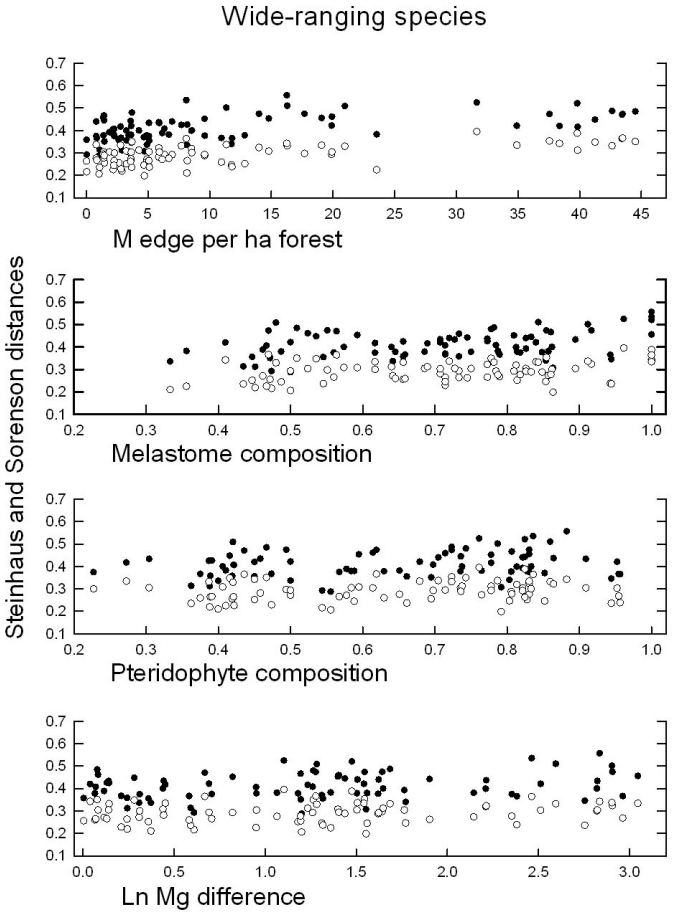

Figure 7.4. Steinhaus (black dots) and Sørenson (white dots) community compositional difference between all 78 possible site pairs. Indices were calculated including only those species whose range maps included all 13 sites. The x-axis shows difference between site pairs in the variable indicated. The forest edge-to-area ratio was measured within 4 km of survey sites, and Melastome and Pteridophyte compositional differences were estimated with the Sørenson index. Associated Mantel correlations are given in Table 7.1 for Mg concentration and Table 7.4 for Melastomes and Pteridophytes, and Figure 7.6 for the fragmentation variable. There were additional variables significantly associated with composition of wide-ranging species, but those shown here were the most important.

Table 7.5. Species found in Indicator Species Analysis to have been disproportionately distributed between survey sites of two different floristic classes. Seven sites had Melastomataceae species compositions indicative of nutrient-rich soil conditions, and six had species compositions indicative of nutrient-poor soils. Indicator value (IV) ranges from 0 to 100, where 100 represents perfect fidelity to one group and representation at every site in that group.

Species	Nutrient group	IV	P
Xiphorhynchus guttatus	rich	66	<0.01
Attila spadiceus	rich	85	<0.01
Tangara schrankii	rich	85	<0.01
Capito auratus	rich	59	<0.05
Eubucco richardsoni	rich	71	<0.05
Ramphastos vitellinus	rich	67	<0.05
Campephilus melanoleucos	rich	82	<0.05
Rhegmatorhina melanosticta	rich	71	<0.05
Tolmomyias poliocephalus	rich	78	<0.05
Chiroxiphia pareola	rich	85	<0.05
Psarocolius decumanus	rich	68	<0.05
Clypicterus oseryi	rich	77	<0.05
Cacicus haemorrhous	rich	69	<0.05
Gypopsitta barrabandi	rich	71	<0.10
Trogon curucui	rich	57	<0.10
Galbula chalcothorax	rich	57	<0.10
Schistocichla schistacea	rich	64	<0.10
Myrmothera campanisona	rich	64	<0.10
Pachyramphus minor	rich	66	<0.10
Turdus albicollis	rich	64	<0.10
Tangara gyrola	rich	64	<0.10
Ocyalis latirostris	rich	57	<0.10
Trogon [melanurus]	poor	100	<0.01
Notharchus ordii	poor	83	<0.01
Dixiphia pipra	poor	81	<0.01
Galbula dea	poor	75	<0.05
Xenops milleri	poor	78	<0.05
Hypocnemis hypoxantha	poor	78	<0.05
Neopipo cinnamomea	poor	67	<0.05
Ramphotrigon ruficauda	poor	79	<0.05
Cyanerpes nitidus	poor	80	<0.05
Conopias parvus	poor	66	<0.10
Tyranneutes stolzmanni	poor	66	<0.10
Schiffornis turdinus	poor	64	<0.10
Cyanerpes cyaneus	poor	57	<0.10

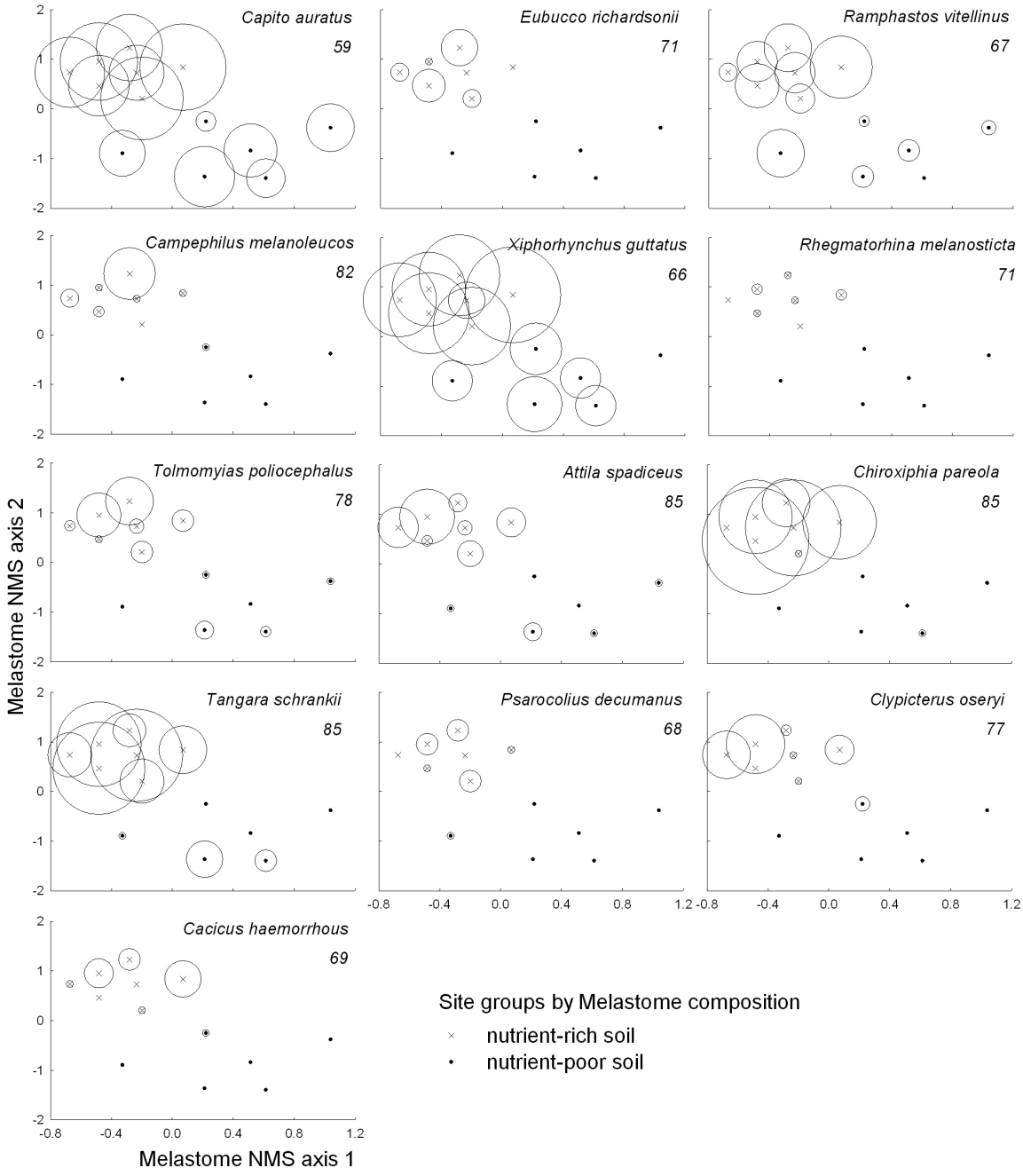

Figure 7.5a. Indicator species analysis for bird species relative abundance differences between two site groups based on Melastomataceae species composition. Axes are the two most important axes from nonmetric multidimensional scaling (NMS) of the floristic data. The size of the circles shows the relative abundance of the bird species on each site. Indicator values are shown below each species name. Species shown here are all those with a significant ($p < 0.05$) indicator value for the nutrient-rich site group.

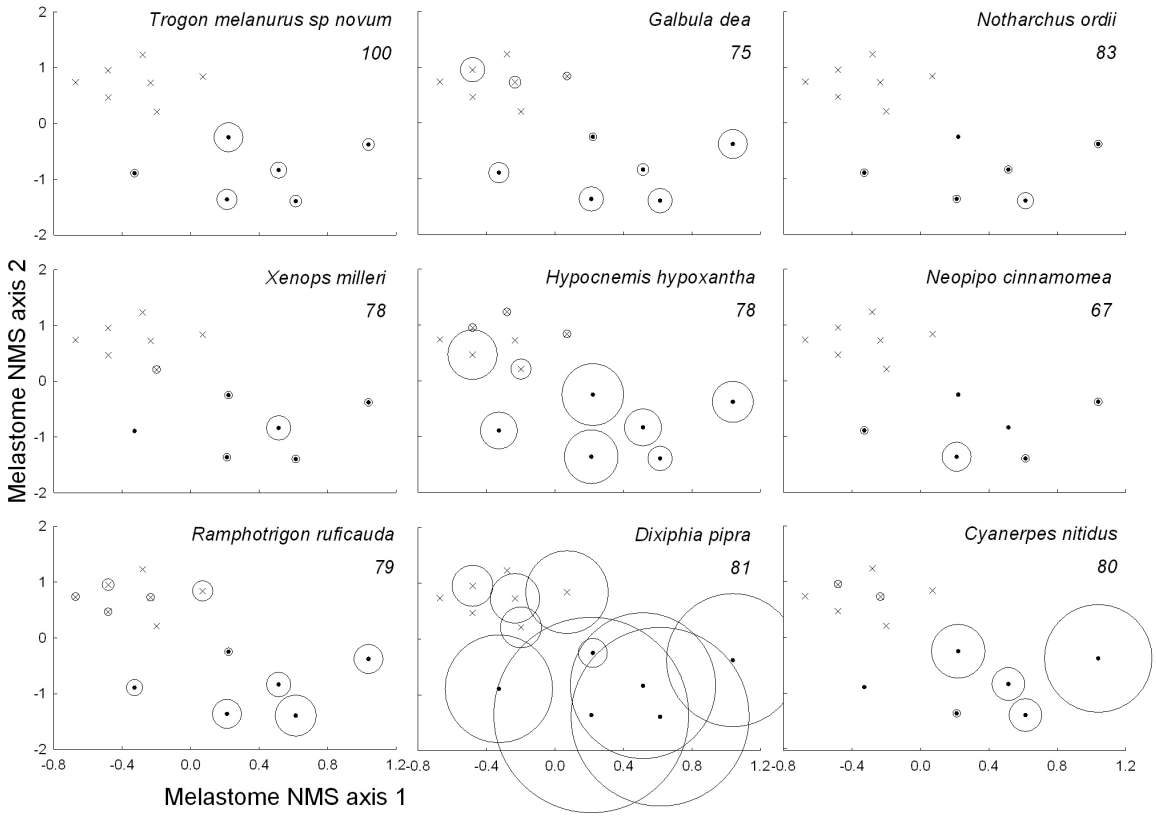

Figure 7.5b. Indicator species analysis for bird species relative abundance differences between two site groups based on Melastomataceae species composition. Species shown here are all those that had a significant ($p < 0.05$) indicator score for the nutrient-poor site group. The NMS ordination used to plot sites according to Melastome composition is the same as that shown in Figure 7.2, although the y axis is inverted here. *Trogon melanurus sp. novum* = *Trogon* [*melanurus*] (see Chapter 9).

Local and landscape forest structure

There was considerable variation among sites in tree basal area, the percentage of transects in early treefall gap phase, and leaf litter depth, while average stand densities were somewhat uniform (Table 7.6). Among all those variables, only small tree basal area was significantly correlated with bird community composition when all species were included, and it was more strongly correlated with genus than with species composition (Table 7.4). When only widespread species were included, the strength of those correlations increased considerably, and stand density of small trees also became weakly correlated with bird species presence, whereas all other forest structure variables remained uncorrelated with bird community composition.

Indicator species analysis was therefore only conducted for basal area of small trees, which was likely indicative of understory and lower midstory foliage densities. There were 12 bird species with a significant indicator value at the $p < 0.05$ level for sites with either higher (five species) or lower (seven species) basal area (Table 7.7). There were 23 species with significant indicator values at the $p < 0.10$ level, of which eight were associated with higher basal area of small stems and 15 with lower basal area.

Variation among sites in landscape-level forest clearing and fragmentation was also pronounced (Table 7.8), although most sites were situated within largely forested landscapes with some localized agricultural deforestation along rivers. The proportion of the landscape covered by mature forest decreased with increasing buffer widths for all

Table 7.6. Vegetation structure variables measured at 13 sites in the Peruvian Amazon. Average basal area and stand density are shown for large (>10 cm diameter at breast height) and small (<10 cm dbh) woody stems at 22 vegetation plots per site, with four trees per plot in each size category. Stand density is the average distance of stems to the vegetation plot center. Treefall gap density is the percentage of the total transect length (2 km) in early gap phase.

Site	Basal area (cm^2)		Stand density (m)		Leaf litter	Treefall gap
	small	large	small	large	(cm)	(%)
ex	12.14	522.8	1.33	2.94	2.9	7
mi	9.12	346.4	0.92	2.84	2.5	32
na	8.43	481.5	1.03	3.06	3.4	8
sp	9.57	514.7	1.07	3.02	3.0	7
sj	8.98	464.3	1.18	2.91	3.4	10
ta	10.67	613.6	1.21	3.02	2.2	12
va	5.96	536.4	1.03	2.97	2.5	8
la	9.07	496.3	1.09	3.03	2.0	15
su	7.40	483.7	0.97	3.33	2.1	6
ne	6.33	564.2	1.02	3.20	2.2	6
np	7.19	519.1	1.16	3.11	1.5	5
hu	7.26	397.1	0.89	3.33	2.8	12
co	7.05	647.0	1.31	2.89	1.5	8

Table 7.7. Species found in Indicator Species Analysis to have been disproportionately distributed between survey sites of two different forest structural classes: those with higher or lower basal area of small trees. Seven sites had small (<10 cm DBH) stem plots with an average basal area above 8 cm^2, and six had an average below 8 cm^2. Indicator value (IV) ranges from 0 to 100, where 100 represents perfect fidelity to one group and representation at every site in that group. Associations between individual species and small stem basal area classes tended to be weaker (lower IVs) than those found for floristic and forest fragmentation classes.

Species	Basal area	IV	P
Zimmerius gracilipes	high	58	<0.05
Hemithraupis flavicollis	high	80	<0.05
Tangara chilensis	high	58	<0.10
Cyanerpes caeruleus	high	70	<0.10
Ocyalis latirostris	high	57	<0.10
Euphonia chrysopasta	high	57	<0.10
Piaya melanogaster	low	70	<0.05
Hypocnemis hypoxantha	low	71	<0.05
Terenotriccus erythrurus	low	61	<0.05
Lipaugus vociferans	low	69	<0.05
Machaeropterus regulus	low	81	<0.05
Saltator grossus	low	70	<0.05
Crypturellus variegatus	low	58	<0.10
Ibycter americanus	low	67	<0.10
Threnetes leucurus	low	54	<0.10
Trogon violaceous	low	62	<0.10
Celeus flavus	low	70	<0.10
Campephilus rubricollis	low	59	<0.10
Philydor pyrrhodes	low	67	<0.10
Automolus infuscatus	low	66	<0.10
Laniocera hypopyrra	low	70	<0.10
Turdus lawrencii	low	64	<0.10

Table 7.8. Landscape-level forest clearing and fragmentation measured at 13 sites in the Peruvian Amazon. Forest area is given as the proportion of the area within the buffer radius for which the land cover was mature forest. The four consecutive numbers in each case are values for 0.5, 1, 2, and 4 km buffer radii, in that order.

Site	Forest area (p)	Forest edge length (km)	Forest edge per hectare
ex	0.80, 0.60, 0.43, 0.51	4.5, 14.3, 40.0, 149.7	25.1, 41.1, 52.3, 49.2
mi	0.97, 0.94, 0.92, 0.92	1.1, 6.2, 18.8, 62.4	5.0, 11.1, 11.4, 11.6
na	0.92, 0.81, 0.83, 0.83	1.6, 6.4, 22.0, 71.6	7.7, 13.4, 14.8, 14.3
sp	1.0, 0.99, 0.90, 0.92	0, 0.4, 17.3, 51.8	0, 0.7, 10.9, 9.4
sj	0.99, 0.99, 0.96, 0.95	0.7, 3.2, 12.3, 26.7	3.4, 5.6, 7.3, 4.7
ta	0.95, 0.92, 0.81, 0.65	1.5, 6.2, 26.1, 101.3	6.7, 11.4, 18.2, 25.6
va	0.93, 0.82, 0.77, 0.69	1.6, 6.1, 28.7, 73.3	7.2, 12.3, 20.6, 17.5
la	0.86, 0.83, 0.89, 0.92	2.7, 7.0, 12.2, 32.1	13.3, 14.0, 7.6, 5.7
su	1.0, 0.96, 0.89, 0.85	0, 3.4, 15.1, 50.4	0, 5.9, 10.2, 10.8
ne	0.95, 0.91, 0.87, 0.89	1.8, 6.8, 25.6, 49.4	8.5, 12.8, 16.7, 9.3
np	1.0, 1.0, 0.98, 0.94	0, 0, 6.2, 43.4	0, 0, 3.6, 7.9
hu	0.93, 0.81, 0.83, 0.83	3.7, 9.6, 22.4, 35.4	16.8, 19.0, 15.1, 6.5
co	0.82, 0.76, 0.70, 0.65	1.7, 3.2, 9.5, 22.3	9.2, 7.2, 7.6, 5.7

sites but Libertad Agraria, which showed the opposite pattern. Forest edge per unit area generally increased with increasing buffer widths for all sites but Libertad Agraria, Huanta, and Constancia. However, among sites where fragmentation generally increased as wider surrounding areas were considered, most sites showed a pattern of increase out to the 2 km buffer width, then a slight decrease at the 4 km width.

Forest clearing and fragmentation measures were highly correlated with bird compositional variation, but only at the widest spatial extents around survey sites (Fig. 7.6, Figures 7.3 and 7.4). Forest area was only correlated with species composition when wide-ranging species were considered separately, whereas forest edge and edge per unit area were strongly correlated with the full species dataset, as well as genus compositions. Those correlations were still strongest, however, when only wide-ranging species were included, and were consistently strongest at the 4 km buffer radius. The amount of forest edge performed as well as edge per unit area at that radius, but at the 2 km buffer radius edge per unit area performed slightly better. Both fragmentation metrics were better predictors of genus turnover than of species turnover when all species were included, and both were more highly correlated with presence data than with abundance data. Because landscapes were classified into two simple classes, mature forest on one hand and open areas plus regenerating forest on the other, values for the two classes were essentially one another's reciprocals. Results are only shown in Fig. 7.6 for forest area, since results for area of open habitats were nearly identical. Forest edge and edge-to-area ratio at the 4 km buffer radius were more strongly correlated with bird species and genus composition than any other local environmental variables.

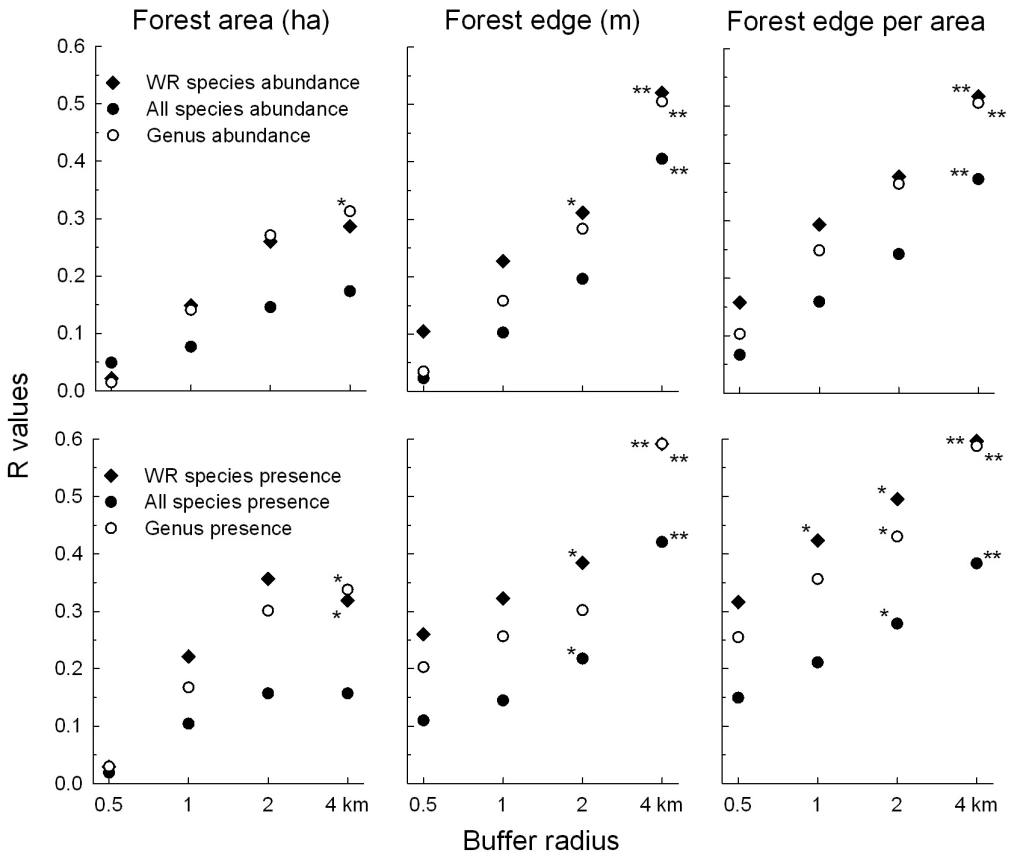

Figure 7.6. Mantel correlation r-values between bird community composition and landscape forest fragmentation at 13 mature forest sites in the Peruvian Amazon. Bird observations were grouped at the species and genus levels, and both abundance (top three charts; Steinhaus index) and presence (bottom charts; Sørenson index) were examined at each taxonomic level. Wide-ranging (WR) species included only those 258 bird species in the survey dataset whose known distributions covered all 13 survey sites. Correlation strengths increased as larger areas of the surrounding landscapes were included. Results for cleared agricultural area were identical to those for forest area. * $P<0.05$; ** $P<0.01$.

For indicator species analysis, I grouped survey sites according to forest edge per unit area at the 4 km buffer radius. There were 17 species with a significant indicator value at the $p < 0.05$ level for sites surrounded by either more fragmented (six species) or less fragmented (11 species) landscapes (Table 7.9). There were 33 species with significant indicator values at the $p < 0.10$ level, of which 11 were associated with more fragmented sites and 22 with less fragmented sites.

Hunting

Iquitos and four smaller towns (Nauta, Tamshiyacu, Indiana, and Pebas) were identified as regional markets where quantities of game meat are sold, and travel time to those markets from survey sites varied from 35 to 590 minutes (Table 7.10). Local community size, travel time to local communities, travel time to regional markets, and the distance to the regional population center of Iquitos all varied widely among survey sites. However, there was no relationship between variation in bird community composition and any of those variables when all species were considered, when individual hunted bird families were considered, or when hunted species were considered as a group (Table 7.11). This was true at the species and genus levels, using both abundance and presence data. Results were not changed when only widespread species were considered.

Table 7.9. Species found in Indicator Species Analysis to have been disproportionately distributed between more fragmented and less fragmented survey sites. Sites were grouped into the five most fragmented and the eight least fragmented, at a 4 km buffer radius. Indicator value (IV) ranges from 0 to 100, where 100 represents perfect fidelity to one group and representation at every site in that group.

Species	Fragmentation	IV	P
Schistocichla leucostigma	High	87	<0.01
Buteo magnirostris	High	85	<0.05
Pionites melanocephalus	High	67	<0.05
Phaethornis malaris	High	75	<0.05
Megastictus margaritatus	High	72	<0.05
Tachyphonus cristatus	High	73	<0.05
Ortalis guttatus	High	54	<0.10
Heliodoxa schreibersii	High	64	<0.10
Pteroglossus pluricinctus	High	65	<0.10
Synallaxis rutilans	High	52	<0.10
Chlorophanes spiza	High	72	<0.10
Tinamus guttatus	Low	86	<0.01
Ibycter Americanus	Low	78	<0.01
Philydor pyrrhodes	Low	80	<0.01
Myrmothera campanisona	Low	88	<0.01
Legatus leucophaius	Low	97	<0.01
Amazona farinosa	Low	75	<0.05
Terenura humeralis	Low	75	<0.05
Schistocichla schistacea	Low	75	<0.05
Dichropogon poecilinota	Low	64	<0.05
Cyanocompsa cyanoides	Low	78	<0.05
Euphonia xanthogaster	Low	73	<0.05
Crypturellus variegates	Low	63	<0.10
Piaya melanogaster	Low	69	<0.10
Pharomachrus pavoninus	Low	70	<0.10
Ramphastos tucanus	Low	61	<0.10
Deconychura stictolaema	Low	69	<0.10
Dichrozona cincta	Low	63	<0.10
Cercomacra cinerascens	Low	68	<0.10
Lophotriccus vitiosus	Low	62	<0.10
Rhynchocyclus olivaceus	Low	65	<0.10
Hylophilus hypoxanthus	Low	57	<0.10
Turdus lawrencii	Low	61	<0.10

Table 7.10. Metrics of hunting accessibility at bird survey transects. Travel times were estimated for the only available or most common mode of transportation, which was normally walking and boat travel, but included road travel for sites near the Iquitos-Nauta highway.

Site	Travel Time (min)		Community size
	Local	Market	(families)
ex	45	95	100
mi	30	240	40
na	35	35	25
sp	40	480	12
sj	100	590	20
ta	120	185	46
va	40	100	60
la	120	175	60
su	40	130	70
ne	20	120	17
np	30	210	12
hu	28	120	185
co	60	360	45

Table 7.11. Mantel correlations (R-values) between bird community composition and metrics for site accessibility, hunting intensity, and forest clearing. Results are presented for tests using abundance data; identical tests using presence data produced similar results. Hunted species included all members of Tinamidae, Cracidae, Odontophoridae, and Psophiidae (a total of 14 species). Parrots (Psittacidae), while not generally hunted for food, are collected for the pet trade. Tinamous were also examined separately because Tinamidae was the most speciose hunted family, with seven species. * $P<0.05$; ** $P<0.01$.

	All		Hunted		Parrots	Tinamous
Variable	Species	Genera	Species	Genera	Species	Species
Local village/town size	0.02	0.02	-0.06	-0.07	-0.05	-0.03
Time to village/town	0.06	0.12	-0.03	-0.04	0.00	-0.06
Time to regional market	-0.06	-0.18	0.00	0.03	0.09	-0.07
Time to Iquitos	0.12	0.15	0.14	0.02	0.14	0.22
Distance to Iquitos	0.12	0.24	0.08	0.01	0.10	0.16
Cleared area, 4 km	0.17	0.31	0.33*	0.32	0.09	0.31*
Forest edge, 4 km	0.41**	0.50**	0.60**	0.60**	0.24**	0.55**
Forest edge per ha, 4 km	0.37**	0.51**	0.55**	0.55**	0.19*	0.49**

On the other hand, the forest clearing and fragmentation metrics were highly associated with variation in the abundance of hunted bird species (Table 7.11). When the families Tinamidae, Cracidae, Odontophoridae, and Psophiidae were considered together, the association with fragmentation variables was stronger than for all bird species as a whole. While the family Psittacidae (parrots) was significantly associated with forest fragmentation variables, the effect was weaker than for bird species as a whole. Results are shown in Table 7.11 for clearing and fragmentation variables measured within 4 km of the survey sites; associations with variables measured at the 2 km buffer radius were usually significant, but much weaker.

Species richness

Estimates of bird species richness by simple count of total observations and by rarefaction were very highly correlated with one another ($r = 0.90$, $p = 0.0001$; Fig. 7.7). There were no significant correlations between variation in plant species richness and topography or soil characteristics, nor were there correlations between bird species richness and any of those variables (Tables 7.3 and 7.12). In fact, the only local environmental variables that were correlated with bird species richness were basal area of small trees and the forest clearing and fragmentation metrics, which were themselves highly correlated. Correlations were uniformly stronger for simple counts of species than for rarefaction estimates. As was the case for bird community composition, correlations between species richness and forest edge increased with increasing buffer radii, and were

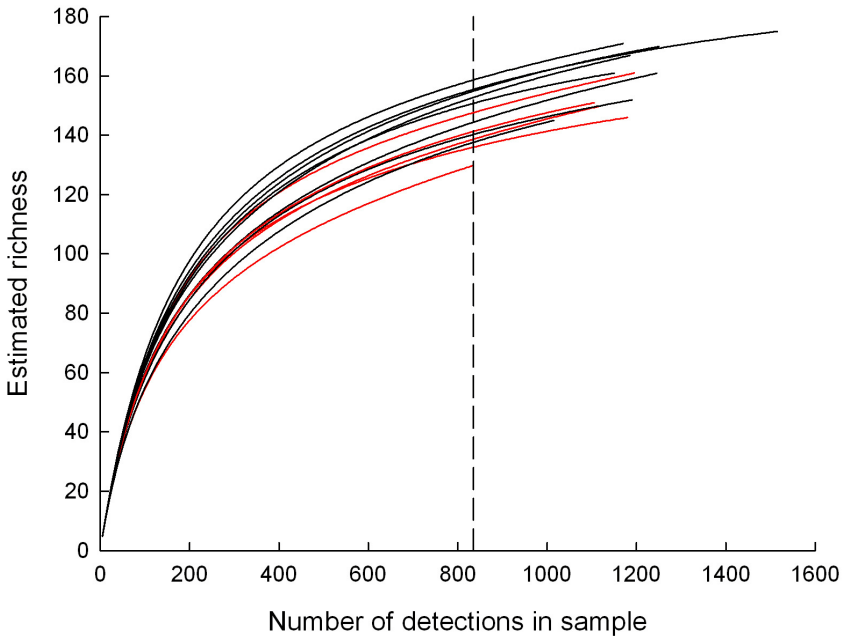

Figure 7.7. Estimation of bird species richness at each of 13 survey sites by rarefaction resampling, with 1000 iterations per sample size. Total expected richness at each site is not projected; rather, relative richness among sites is estimated given constant sample size. Each curve represents a single site, and the dotted line at 839 detections marks the full sample size at Expetroleros, where the fewest detections were made. The tip of each line shows the equivalent of the simple count of species detected, and the total number of individual detections. The five sites with the highest levels of forest fragmentation are shown in red. The curves have not leveled off at the full sample sizes, suggesting that species would likely continue to accumulate with continued sampling.

Table 7.12. Mantel correlation of bird species richness with bird species composition, regions, and environmental variables. R-values are shown for estimates of richness by rarefaction to a standardized sample of 839 individual bird detections per site (839 = total detections at the site with the fewest detections), and for the simple count of all species actually detected including all observations at each site. Those two richness estimates were themselves very highly correlated (R = 0.90, p = 0.0001). Topography results are only shown for elevation range and variance at the 500 m radius around transects; results at other radii were similarly non-significant. Forest area and fragmentation indices are only shown at the 2 km radius around transects; complete results for area and fragmentation effects are shown in Fig. 7.8. * P<0.05; ** 0.001< P <0.010.

	Bird species richness	
Variable	Rarefaction	Simple count
Bird species composition (Sørenson)	0.31*	0.37**
Bird species composition (Steinhaus)	0.20	0.27*
Regions N and S of Amazon	0.10	0.17
Bird species range maps	0.17	0.21*
Count of species from range maps	0.01	0.05
Geographic distance	0.04	-0.07
Geographic distance (ln)	0.10	0.01
Elevation range, 0.5 km radius	-0.04	-0.05
Elevation variance, 0.5 km radius	0.03	0.09
Soil: Ca + K + Mg + Na (ln)	-0.08	-0.06
Soil: Loss on Ignition (ln)	0.02	-0.11
Soil: Clay, silt (ln)	-0.14	-0.15
Soil: pH	-0.13	-0.11
Melastome species composition	-0.12	-0.11
Melastome species richness	0.23	0.28
Pteridophyte species composition	-0.01	0.01
Pteridophyte species richness	-0.09	-0.07
Treefall gap proportion	-0.11	-0.15
Stand density (>10 cm DBH)	0.08	-0.02
Stand density (<10 cm DBH)	0.08	0.21
Basal area (>10 cm DBH)	-0.18	-0.10
Basal area (<10 cm DBH)	0.28*	0.38*
Forest area proportion, 2 km radius	0.30	0.52*
Forest edge length, 2 km radius	0.37*	0.51**
Forest edge-to-area ratio, 2 km radius	0.39*	0.59*
Distance to nearest community (min)	-0.15	-0.14
Size of nearest community (families)	0.07	0.08
Distance to regional market (min)	-0.16	-0.14
Distance to Iquitos (min)	-0.03	-0.03

quite strong at the 4 km radius (Fig. 7.8). Correlations with the edge to area ratio were slightly weaker, and dropped off slightly at the 4 km radius. Species richness was more strongly correlated with forest area than was species composition, and unlike the fragmentation metrics, the correlation with area was significant at the smaller buffer radii then disappeared at the 4 km radius. While all these patterns appeared to be similar between simple species counts and rarefaction estimates, rarefaction estimates only showed statistically significant correlations with the fragmentation metrics at the 2 km and 4 km buffer radii (Fig. 7.8).

The simple count of richness, but not the rarefaction estimate, was weakly correlated with bird species composition using the Steinhaus abundance index. Both richness estimates were more strongly correlated with species composition using the Sørenson presence index. Neither estimate was correlated with geographic distance among sites or with regions north and south of the Amazon River, but the simple count of richness was very weakly correlated with site-to-site variation in bird species composition according to species range maps. Variation in species richness as measured during site surveys was not correlated with variation in species richness as expected from range maps (Table. 7.12).

Correlations among independent variables

Independent environmental variables that were significantly associated with bird community composition were not correlated with one another, with the following

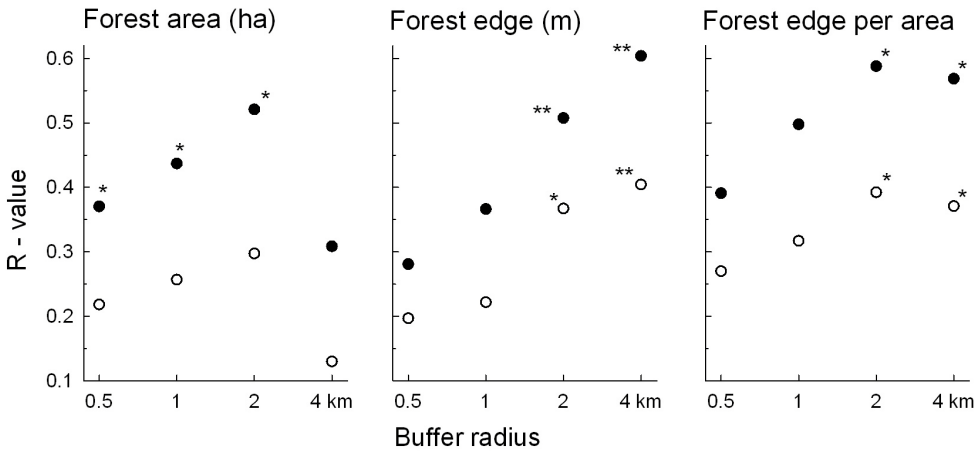

Figure 7.8. Mantel correlation r-values between bird species richness and landscape forest fragmentation across 13 survey sites. * P<0.05; ** P<0.01. Dark circles represent r-values resulting from simple counts of species detected at each site, and hollow circles represent r-values when species richness is estimated by rarefaction to 839 samples per site. High species richness was generally associated with low levels of landscape-level forest fragmentation. Unlike bird species composition, bird species richness was also associated with forest area, at least when simple species counts were used. Results for cleared area were identical to those for forest area, since the two metrics were essentially one another's reciprocals.

important exceptions. Small stem basal area was highly correlated with both forest edge ($r = 0.61$, $p = 0.01$ at the 4 km radius, $r = 0.42$, $p = 0.03$ at the 2 km radius) and the forest edge to area ratio ($r = 0.65$, $p = 0.01$ at the 4 km radius, $r = 0.58$, $p = 0.02$ at the 2 km radius). In partial Mantel tests controlling for small stem basal area, forest edge at 4 km remained significantly correlated with bird species and genus composition ($r = 0.38$, $p = 0.01$ and $r = 0.44$, $p = 0.06$, respectively) using presence data; results were similar using abundance data. Small stem basal area, on the other hand, was not correlated with either species or genus composition when controlling for forest edge ($r = -0.06$, $p = 0.68$ and $r = 0.15$, $p = 0.24$, respectively) using presence data; results were again similar using abundance data. Results were also similar when the forest edge to area ratio was used in place of forest edge. Large stem (> 10 cm DBH) basal area was not correlated with the amount of forest edge ($r = 0.08$, $p = 0.48$ at the 4 km radius, $r = -0.17$, $p = 0.19$ at the 2 km radius) or the edge to area ratio.

Elevation variance at 2 km was negatively correlated with the single most important deforestation measure, the length of mature forest edge within 4 km of transects ($r = -0.19$, $p = 0.04$). Although that correlation was very weak, it did appear that the sites with the highest levels of forest fragmentation were of middling hilliness, with the flattest and hilliest sites being distant from Iquitos and showing little forest fragmentation. It is likely that the weak, negative correlation between elevation variance at 2 km and bird community composition was an artifact of the correlation of the fragmentation variable with both elevation variance and community composition.

Finally, plant species compositions were very strongly correlated with multiple edaphic variables, as shown in Table 7.3. While Melastome composition was associated with bird species composition, soil variables were not associated with bird species compositions when all bird species were considered. However, when only wide-ranging species were considered, cation concentrations were associated with species composition, and associations between bird and plant species compositions became more pronounced (Tables 7.1 and 7.4). In partial Mantel tests controlling for Mg concentration, Melastome composition remained significantly associated with wide-ranging bird species composition ($r = 0.27$, $p = 0.05$ for abundance data; $r = 0.28$, $p = 0.05$ for presence data). However, controlling for Melastome composition, there was no longer a relationship between Mg concentration and wide-ranging bird species composition ($r = 0.05$, $p = 0.33$ for abundance data; $r = -0.03$, $p = 0.47$ for presence data). This pattern was similar for the remaining cation variables and for the summed cations variable, which were more weakly associated with bird composition.

DISCUSSION

In general, the environmental variables that were strongly correlated with avian community composition related to forest structure at local and landscape scales, and to floristic composition and associated soil characteristics. Bird species richness was correlated only with local and landscape-level forest structure characteristics. Important associations, including those between avian composition and soil cation concentrations,

floristic composition, basal area of small trees, and forest fragmentation indices, were consistently stronger at the genus level than at the species level when all species were included in analyses. This may be primarily an artifact of species versus genus range limits, and in particular, the division of the study area into sites to the north and south of the Amazon River. When only wide-ranging species were considered, the strengths of their associations with environmental variables were comparable to those at the genus level.

Bird species composition was very different on opposite sides of the river, as was genus composition, but the difference was less pronounced at the genus level. A good deal of difference between the two regions is accounted for by species with distributional limits at the river, and those distributional limits are apparently not correlated with environmental differences, as discussed in the previous chapter. Therefore, when local habitat associations were examined, many species' absence from multiple survey sites due to distributional limits tended to statistically weaken local habitat associations that may have existed where the species was present. There was, for example, a maximum of seven survey sites inside the known distributions of species restricted at the Amazon River, a sample size that may be inadequate for detecting community composition correlations with matrix analyses. The problem is actually compounded, because species restricted to one side of the river were recorded as absent from all sites on the opposite side of the river, resulting in a dilution of any habitat association that may have been evident on the occupied side of the river. Habitat associations were not examined within

northern and southern regions separately, due to the small number of study sites within either region.

If this problem can explain at least part of the discrepancy between local habitat associations at the all-species and genus levels, then it is probable that the results for wide-ranging species are actually more indicative of general patterns for all species, since there is no particular reason to suspect that more range-restricted species are less likely to be habitat specialists, or to be less responsive to the particular environmental variables I measured. In fact, there were multiple range-restricted species that, while they did not show local habitat associations in this study, are known to be associated with particular terra firme habitats, and I discuss those species below.

Soils and topography

Topographic measures were found to be generally unimportant as predictors of bird or plant composition or richness, whereas soil nutrient characteristics were important. I did not sample extremely nutrient-poor or extremely nutrient-rich sites, relative to the range of reported values in Loreto and adjacent Ecuadorian Amazonian sites (Ruokolainen and Tuomisto 1998, Tuomisto et al. 2002, Tuomisto et al. 2003b). Nonetheless, there were correlations between soil nutrient concentrations and both plant species and bird species composition, and the compositional variation in plant species with edaphic variation was especially pronounced. The lack of correlation between species richness of either Pteridophytes or Melastomes and cation or other soil characteristics, on the other hand,

was likely due to the fact that I sampled an intermediate range of soil nutrient values within which relatively little change in plant species richness has been observed in past studies (Tuomisto et al. 2002).

Since indeed floristic effects, in terms of both species composition and richness, are more pronounced across the whole range of edaphic gradients seen in western Amazonian terra firme habitats, correlations between floristics and bird community composition may also be significantly more pronounced than those I documented. In fact, this should be obvious at the nutrient-poor extreme of the edaphic gradient, considering the well-known white-sand forests that I did not sample, but that are known to be unusually distinctive in bird and plant composition. Somewhat less obviously, bird communities in forests growing on significantly more nutrient-rich soils than the sites I sampled, such as those in Yasuni National Park in Ecuador, may eventually be found to be more different from white-sand and other nutrient-poor forest communities than were any of the sites sampled in this study.

Floristic associations

Most of the bird species with significant indicator values for the nutrient-poor floristic class have been described in the literature as specialized to some degree on sandy-soil, nutrient-poor Amazonian forest habitats, but specialization on the more widespread clay-soil, nutrient-rich Amazonian habitats has been less well studied.

The composition of species distributed on both sides of the river, and wide-ranging species in general, was more strongly correlated to both Pteridophyte and

Melastome composition than was species composition including all bird species. Thus, the widely-distributed species were primarily responsible for observed correlations between bird and plant composition. This is confirmed by indicator species analysis, for which all species showing significant associations with one of the floristic groups were widely distributed species. This is probably an artifact of effectively reduced sample size for species that were range-restricted within the study area, and does not necessarily suggest that wide-ranging species are more likely to be habitat specialists.

There are a number of species that occurred in the dataset, and that are known to be strongly associated with forests growing on nutrient-poor, sandy soils, but that were not identified herein as indicators of that floristic forest type. These were species with limited distributions in the study region, whose ranges did not include more than a few survey sites, and so for whom valid statistical tests of habitat association across the study sites were not possible. Species in this category, including *Herpsilochmus gentryi*, *Percnostola arenarum*, *Neopelma chrysocephalum*, *Xipholena punicea*, and *Polioptila clementsi*, were each detected at only one or two survey sites, always nutrient-poor soil sites, and are well-documented as specialists on that habitat (Whitney and Alvarez 1998, Isler et al. 2001, Alvarez 2002, Alvarez and Whitney 2003, Whitney and Alvarez 2005).

Thus, in terms of habitat association, the true strength of spatial correlation between floristic and avian community composition is probably most accurately represented by the comparison of plant species to widely distributed bird species. An analysis including a large number of survey sites on only one side of the river would likely result in a generally higher correlation between bird and plant taxonomic

composition. Nonetheless, the dilution of that correlation by species distribution limits, at the river and elsewhere in the study area, is meaningful. It suggests that regional distribution limits are very different in birds than in plants in the western Amazon, and this difference diminishes the utility of ecoregions as highly general descriptors of biogeographic diversity across all taxa.

Forest structure associations

Forest edge and the edge to area ratio were more statistically important variables than basal area at the community level. It may still have been the case, however, that small stem basal area was a functionally important variable for some bird species, particularly those that forage in the understory and midstory. One can speculate that small stem basal area was positively correlated with forest edge in surrounding landscapes because the higher accessibility of fragmented forests has led to higher rates of selective timber harvest and other activities by local people, but there was no way to determine such a relationship using the data available in this study. Indeed, none of the statistical associations demonstrated in this study are conclusive with regard to functional ecological associations, and the intercorrelated stem size and forest fragmentation variables might best be considered to be collectively indicative of a generally strong response of multiple bird species to various alterations in forest environments near anthropogenic forest edges. It is likely that some functionally important alterations were not measured at all in this study. At the same time, the stem size and fragmentation

variables were associated with nearly completely different species groups (Tables 7.7 and 7.9), and it is likely that different species responded individualistically to different anthropogenic changes.

Many of the species associated with fragmented sites in this study are widely recognized as being associated with forest edge or secondary forest habitats, while several of those associated with unfragmented sites have been noted in the literature as being edge-sensitive, forest interior birds. As was the case for floristic associations, there were a number of species detected at only a few sites that did not therefore show statistical associations with forest structure variables, but that are nonetheless known to be primarily associated with forest edge, canopy openings, secondary forest, and open habitats (Hilty and Brown 1986, Ridgely and Tudor 1989, 1994, Ridgely and Greenfield 2001, Schulenberg et al. 2007). Those species were typically detected only a few times at sites in the most fragmented forest landscapes, especially the Expetroleros and Tarapoto sites. They included *Crypturellus soui*, *Daptrius ater*, *Glaucidium brazilianum*, *Pteroglossus castanotis*, *Tolmomyias flaviventris*, *Poecilotriccus capitalis*, *Megarhynchus pitangua*, *Tyrannus melancholicus*, *Tityra semifasciata*, *Tangara mexicana*, and *Saltator maximus*.

Those species occasionally entered forest interior when it was not distant from more open habitats, or when it had been disturbed by resource extraction or wind events. Unlike the case of floristic associations, these were not primarily species with limited distributions in the study region, but rather tended to be widespread species (although *Poecilotriccus capitalis* does not range south of the Amazon River) that were only

detected at a few sites in fragmented landscapes. Nonetheless, removing range-restricted species did strengthen the statistical associations between forest and landscape structure variables and bird species composition. Range-restricted species tended not to show statistical associations with environmental variables due to the sampling issue discussed above, and removing them from analyses had the effect of increasing the proportion of the remaining species that did show associations with forest structure.

Forest physiognomy and floristics

Both floristic and structural variables were correlated with bird community composition. At both the species and genus levels, floristic composition appeared to be more important than local forest structure, but less important than landscape composition and fragmentation. However, the groups of species that showed associations with floristic composition on one hand, and structural variables on the other, were almost entirely distinct, suggesting that the relative importance of floristic and physiognomic factors at the community level should be understood not so much as an outcome of the influences of both factors on individual species, but rather as an outcome of individual species' responses to either one or the other factor. That is, species with strong associations with one or the other floristically defined habitat were not, in general, responsive to physiognomically defined habitats, and vice versa.

Species richness was associated with forest structure characteristics, primarily at landscape scales, but not with floristic composition. Sites surrounded by landscapes with

high levels of forest clearing and fragmentation tended to have lower numbers of bird species, in accord with most fragmentation studies. While it is known that forests growing on extremely impoverished soils (white sands) in Loreto can have low species richness, this effect was not expressed within the more limited range of soil nutrient conditions and floristic compositions sampled in this study.

Hunting and other anthropogenic factors

There were no associations detected between bird community composition or species richness and any of the variables that were intended to represent the accessibility of sites and the sizes of local human populations, which should be associated with hunting intensity and other indirect influences on forest habitats. In particular, bird species that are commonly hunted, and that were commonly seen to be hunted in and around the survey sites during this study, did not show measurable variations in this regard.

This seems to contradict evidence from the forest fragmentation measurements, which showed strong correlations with bird species and genus turnover, and which also represent the influence of local human populations via agricultural clearing. However, the forest clearing and fragmentation measurements were not statistically associated with the hunting intensity variables. Indeed, the Huanta site was within close walking distance of the community of Huanta, which was larger in population than any other site's nearest community, yet there was extremely little forest fragmentation near the Huanta site. Conversely, the Tarapoto site was surrounded by a landscape with high levels of forest

fragmentation, even though Tarapoto was a relatively small community, and the site was several hours walking distance from the village center.

There are several factors that may contribute to the unpredictable relationship between forest fragmentation, distances from human settlements, and human population sizes. Chief among these is the suitability of different sites for village centers and for agriculture. While these areas need to be relatively near one another at fairly large spatial scales, people typically have large areas around villages within which to locate agricultural activities, and some places are better than others. In particular, village centers are often located near or at a riverbank, chiefly for transportation purposes, while desirable agricultural land may either be near the river or far from it. Poor soils were avoided in some cases, such as Huanta, where the survey site was located in a sandy-hilly area and agriculture was concentrated on the opposite side of the village and across the river, where soils were known to be better. This was not, however, always the case—forest fragmentation was relatively high at the Nauta site despite very sandy-hilly conditions, most certainly because the site was very near the recently paved Iquitos-Nauta road.

Thus, distances from human settlements and the sizes of those settlements may not be good indicators of human activity in particular forest locations in the landscapes around those settlements. Agricultural clearing and associated forest fragmentation arguably provide a better indication of areas where people may be entering forests to hunt and gather forest products, since they are at least definitely using those places to grow crops. In fact, site-to-site variation in the forest fragmentation metrics was highly

associated with variation in the abundance of hunted bird species, even more so than with all bird species in general or with all wide-ranging species. While this unusually strong relationship suggests that hunted species were persecuted near agricultural areas, other effects not related to hunting cannot be ruled out. In particular, it should be noted that *Ortalis guttata*, the Speckled Chachalaca, belongs in Cracidae and is an edge-associated bird that actually showed higher abundances at more fragmented sites. Other hunted species tended to be less common at more fragmented sites, particularly the most common terra firme Tinamou at the study sites, *Tinamus guttatus*, the White-throated Tinamou.

Chapter Eight

Modeling Avian Beta Diversity with Regional and Environmental Variables

RESULTS

Regional patterns

Bird species distribution maps and the simple regional designation defined by the Amazon River were, of all the variables considered, the most strongly correlated with avian species composition, and those two variables were also strongly correlated with one another (Tables 8.1, 8.2, and 8.3). Results using abundance data were remarkably similar to those using only presence data. These factors explained species composition variability primarily due to the large number of species with range limits at the Amazon River, but also due to species with relative abundance differences between sides of the river. A small number of species with distributional limits that lay within the study region, but that were not described by the river, also contributed to the correlation between range maps and species composition.

Those patterns were reinforced by Indicator Species Analysis, which identified 31 species restricted to sites on one side of the river (Table 5.4). An additional 28 species

Table 8.1. Mantel correlations (R-values) between bird community composition and predictor variables entered in multiple regression models. Associations shown here are for all species and genera. Each comparison was made using relative abundance information as well as presence information. No tests were conducted for taxon distributions (range maps) at the genus level. All tests were partial Mantels, wherein variability associated with the natural logarithm of geographic distance was partialled out (for this reason, r-values may vary slightly from those given in the preceding two chapters). * P<0.05; ** P<0.01; *** P<0.001.

	Abundance (Steinhaus index)		Presence (Sørenson index)	
Regional	Species	Genera	Species	Genera
ln distance	0.28*	0.19	0.21	0.10
Region (N or S of Amazon)	0.73**	0.31**	0.74***	0.21*
Species range maps	0.79***	~	0.81***	~
Local				
Floristics (Melastomataceae)	0.32*	0.38**	0.30*	0.30*
Basal area <10 cm	0.25*	0.45**	0.21*	0.46*
Forest edge within 4 km	0.43**	0.52**	0.44**	0.60**
Forest edge/area within 4 km	0.40**	0.52*	0.40**	0.60**

Table 8.2. Mantel correlations (r-values) between bird community composition and predictor variables entered in multiple regression models. Associations shown here are for wide ranging species, i.e., only those 258 species in the dataset whose ranges included all 13 survey sites. Each comparison was made using relative abundance information as well as presence information. * P<0.05; ** P<0.01; *** P<0.001.

	Abundance (Steinhaus index)	Presence (Sørenson index)
Regional	WR Species	WR Species
ln distance	0.17	0.11
Region (N or S of Amazon)	0.38**	0.28**
Species range maps	0.47***	0.39***
Local		
Ca	0.19*	0.16
Mg	0.27*	0.19
Na	0.25*	0.15
Ca+K+Mg+Na	0.23*	0.17
Pteridophytes	0.22*	0.15
Melastomataceae	0.37**	0.33*
All plant species	0.31**	0.25*
Basal area <10 cm	0.40*	0.43**
Stem dens <10 cm	0.21	0.27*
Percent forest area within 4 km	0.29	0.32*
Forest edge within 4 km	0.52**	0.59**
Forest edge/area within 4 km	0.52**	0.60**

Table 8.3. Mantel correlations (R-values) among those regional and local environmental variables previously determined to be correlated with bird community composition at 13 survey sites. Regions were north and south of the Amazon River. Sm. basal and Sm. dens. refer to basal area and stem density, respectively, of stems <10 cm DBH. Forest area and fragmentation metrics are shown for the 4 km buffer radius. Metrics at the 2 km and 4km radii were highly correlated, and the 4 km variables were always retained in the final regression models. Similarly, of the soil and floristic variables that were highly intercorrelated, Melastome composition was always retained in the models. * P<0.05; ** P<0.01; *** P<0.001.

	Regions	Maps	Ca	Mg	Na	Cations	Ferns	Mel	F+M	Sm basal	Sm dens	For area	For edge	E/Area
Ln distance	0.2	0.4**	-0.05	-0.11	-0.20	-0.09	-0.13	-0.11	-0.13	0.11	-0.04	-0.08	-0.03	-0.05
Regions	1.0													
Rangemaps	0.95***	1.0												
Ca	-0.07	-0.08	1.0											
Mg	-0.08	-0.11	0.72***	1.0										
Na	0.13	0.06	0.45**	0.47**	1.0									
Ca+K+Mg+Na	-0.06	-0.08	0.97***	0.78***	0.48**	1.0								
Ferns	-0.01	-0.04	0.75***	0.82***	0.53**	0.78***	1.0							
Melastomes	0.05	0.02	0.66***	0.63**	0.65***	0.65**	0.71***	1.0						
Fern+mel	0.03	-0.01	0.76***	0.79***	0.63***	0.77***	0.94***	0.91***	1.0					
Sm. basal	-0.08	0.03	0.10	-0.06	-0.04	0.01	-0.02	0.03	0.00	1.0				
Sm. dens.	-0.10	-0.09	0.39**	0.41**	0.13	0.44**	0.44**	0.33*	0.42**	0.17	1.0			
Forest area	-0.05	-0.03	0.05	0.13	-0.08	0.08	0.05	-0.01	0.01	0.43*	0.45**	1.0		
Forest edge	0.09	0.15*	0.08	0.04	-0.06	0.11	0.04	0.00	0.02	0.61**	0.35*	0.67**	1.0	
Edge/area	0.03	0.09	0.06	-0.03	-0.07	0.08	-0.02	-0.03	-0.04	0.65**	0.35*	0.71**	0.97***	1.0

were present on both sides, but showed significant abundance differences between sides at the $p<0.05$ level (47 species at the $p<0.10$ level). Significantly, 13 of the latter 28 species contained previously described, allopatric subspecies that replace one another on opposite sides of the river.

Regions were far more weakly correlated with genus composition, but the correlation was nonetheless significant, and was stronger when abundance data were used than when only presence data were used (Table 8.1). Generalized genus distribution maps were not considered for analysis. The weaker taxonomic distinction between regions at the genus level than at the species level can be attributed to the large number of genera that are distributed on both sides of the Amazon, but some or all of whose species are restricted to one region.

Species range maps were highly correlated with regions, as expected (Table 8.3). Separate regression models were built using only one of the two, because there were conceptual and practical reasons for using each. The range maps represent the cumulative influence of a large number of known and unknown, and here unmeasured, biogeographic factors on individual species distributions, and therefore they do not represent a well-defined hypothesis explaining beta diversity. However, they do represent concrete existing knowledge of species distributions that may be used for predictive modeling and mapping purposes, and their potential utility for conservation planning should not be ignored. On the other hand, the Amazon River is a landscape feature independent of species distributions and potentially exerting a strong influence upon them, and as such

fits well in a mechanism-driven modeling framework with other independent landscape variables.

The natural logarithm of geographic distance (distances among sites) was weakly correlated with species composition, but only when abundance data were used, and it was not correlated with genus composition. It was therefore included as a candidate variable for regression models, but was not retained in any model.

Local environmental patterns

The species composition of Melastomes, but not that of ferns, was significantly correlated with bird species and genus composition, and the correlations were slightly stronger when bird abundance data were used (Table 8.1). The strengths of correlation between Melastomes and bird species, and between Melastomes and bird genera were fairly similar. Indicator species analysis identified nine bird species associated with the group of sites containing nutrient-poor soil Melastome communities at the $p < 0.05$ level, and 13 species at the $p < 0.10$ level. Thirteen additional species were associated with the group of sites containing nutrient-rich soil Melastome communities at the $p < 0.05$ level, and 22 species at the $p < 0.10$ level (Table 6.5, Fig. 6.5).

Among the forest structure variables, only the basal area of small trees (<10 cm DBH) was significantly correlated with community composition. Results were extremely similar using abundance or presence data, and the association was stronger at the genus level. Indicator species analysis identified only two species that were associated with

high small tree basal area at the $p < 0.05$ level, and six at the $p < 0.10$ level. Six species were associated with low small tree basal area (and probably a correspondingly more open midstory) at the $p < 0.05$ level, and 16 species at the $p < 0.10$ level (Table 6.7).

Among the landscape composition variables, forest edge and forest edge-to-area ratio were strongly correlated with community composition at the widest (2 km and 4 km) radii. Those two fragmentation metrics were strongly inter-correlated, as were the buffer radii, within metrics. Each metric was more strongly correlated with genus composition than with species composition, and each was more strongly correlated with species and genus composition at the 4 km radius than at the 2 km radius. Due to the very strong correlation between the two radii, only variables calculated at the wider radius were included as model input variables. Five species were associated with high levels of forest fragmentation at the $p < 0.05$ level, and eight species at the $p < 0.10$ level. Seven species were associated with low levels of forest fragmentation at the $p < 0.05$ level, and 15 species at the $p < 0.10$ level (Table 6.8).

Small tree basal area and the two landscape fragmentation metrics were also highly correlated with one another (basal area vs. edge/area at 4 km radius: $r = 0.65$, $p = 0.005$; Table 8.3). The two fragmentation metrics at the 4 km radius were the most strongly correlated with community composition, but all three variables were nonetheless included as model input variables. This was done because an ecological or human land-use mechanism explaining the relationship between high forest fragmentation and high density of small trees was speculative at best, and it was considered likely that the two

could affect different forest bird species in different ways. This was supported by the very low overlap in the specific species whose abundances varied with fragmentation vs. basal area (Tables 6.7, 6.8)

No human influence variables other than the anthropogenic forest edge metrics were included as candidate variables, because none were significantly correlated with avian community composition. There was a marginally significant correlation between travel time to regional markets and hunted species composition, but it was not significant at the level of the whole bird community. Thus, the complete list of model candidate variables included only those variables presented in Tables 8.1 and 8.2, for all species and for wide ranging species, respectively.

Combined patterns

Strong models were obtained from the multiple regression analyses for both abundance and presence datasets, at the species and genus levels, although the genus-level models did not perform as well as the species-level models (Table 8.4, Figures 8.1, 8.2, and 8.3). Nearly 82 percent of the variability in species abundances could be accounted for by a combination of range maps (by far the most important variable), the edge-to-area forest fragmentation metric, and Melastome composition, in descending order of importance. This model remained nearly unchanged when only presence data were used, and was only slightly weaker when regions defined by the Amazon River were used in place of range maps. The same variables (regions, forest fragmentation, and Melastome composition)

Table 8.4. Results of species-level and genus-level multiple regression models, using forward selection then backward elimination. Separate models were built for abundance and presence data, as well as for species distribution maps and the regional distinction, north or south of the Amazon River. Wide-ranging (WR) species models were those for which the dependent matrix only included the 258 species whose known ranges extended across all 13 study sites. AM = abundance data, rangemaps; PM = presence data, rangemaps; AR = abundance data, river; PR = presence data, river. No models were constructed using distribution maps at the genus level. The same three variables were consistently retained in all models, though their order of importance varied: a regional variable (maps or river, whichever was included as a candidate variable), the forest edge/area ratio at the 4 km radius (frag), and Melastome species composition (mel). Abundance and presence data yielded very similar results.

Level	Data	Regression on matrices model	R-squared	P
All species	AM	(0.77) maps + (0.31) frag + (0.27) mel	0.817	0.001
	PM	(0.78) maps + (0.32) frag + (0.26) mel	0.825	0.001
	AR	(0.68) river + (0.37) frag + (0.27) mel	0.773	0.001
	PR	(0.74) river + (0.37) frag + (0.24) mel	0.763	0.001
WR species	AM	(0.49) frag + (0.41) maps + (0.38) mel	0.581	0.001
	PM	(0.58) frag + (0.34) mel + (0.30) maps	0.566	0.001
	AR	(0.52) frag + (0.37) mel + (0.34) river	0.529	0.001
	PR	(0.60) frag + (0.34) mel + (0.21) river	0.520	0.001
Genera	AR	(0.51) frag + (0.36) mel + (0.29) river	0.481	0.001
	PR	(0.59) frag + (0.29) mel + (0.19) river	0.472	0.001

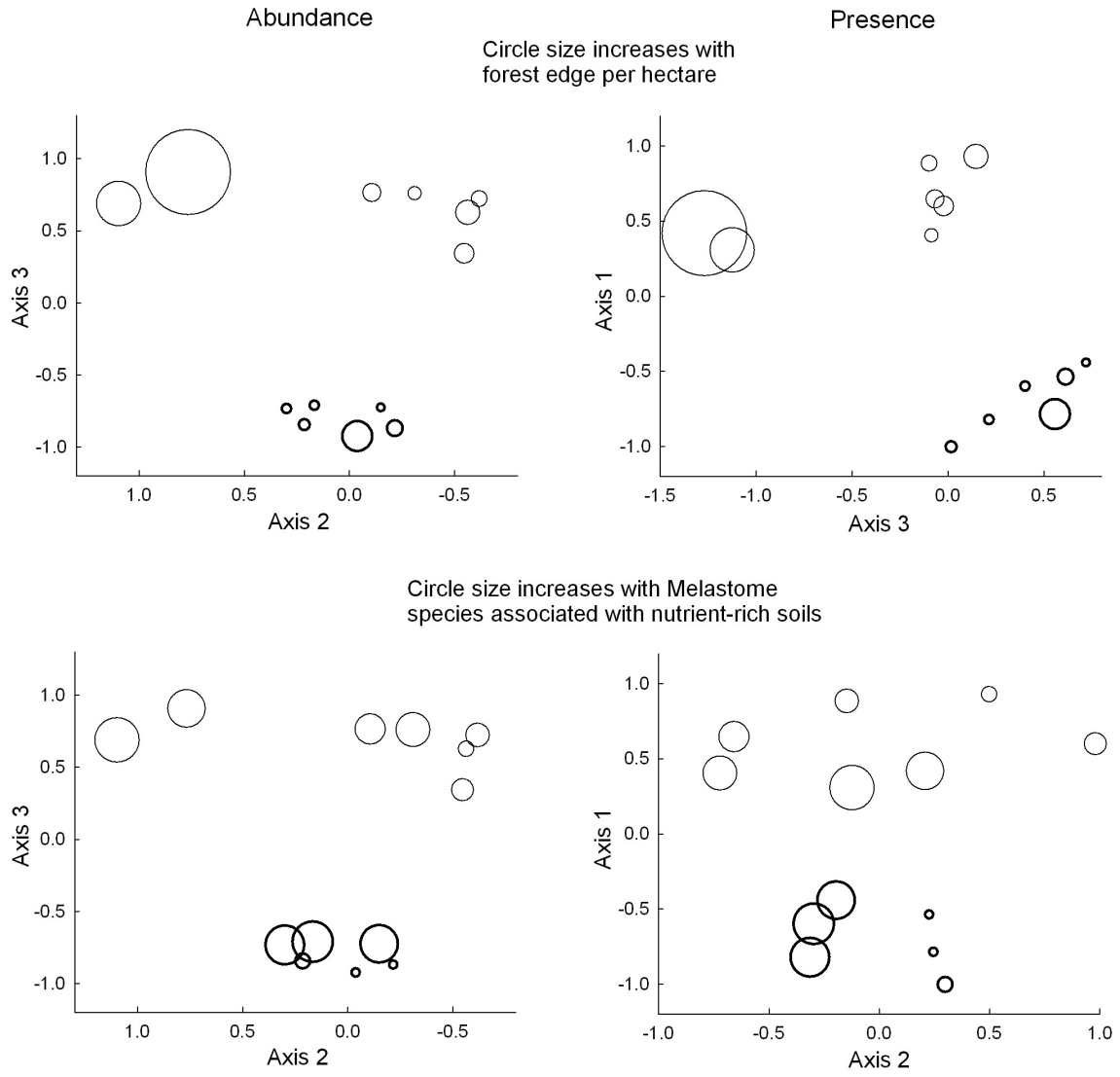

Figure 8.1. Nonmetric multidimensional scaling (NMS) ordinations of 13 bird survey sites, where distance among circle centers is proportional to bird species compositional difference. This ordination included all species, using abundance data (left) or presence data (right). Light and dark circles represent sites north and south of the Amazon River, respectively. In the top two plots, the horizontal axis was correlated with forest fragmentation at the 4 km radius, and the vertical axis with the north/south regional distinction. Circle size is proportional to the degree of forest fragmentation. In the bottom two plots, the horizontal axis was correlated with Melastome species composition, and the vertical axis with regions. Circle size is proportional to the most important axis of an NMS ordination of Melastome species composition. NMS axis signs are arbitrary, and axes are oriented to show similarities among the graphs.

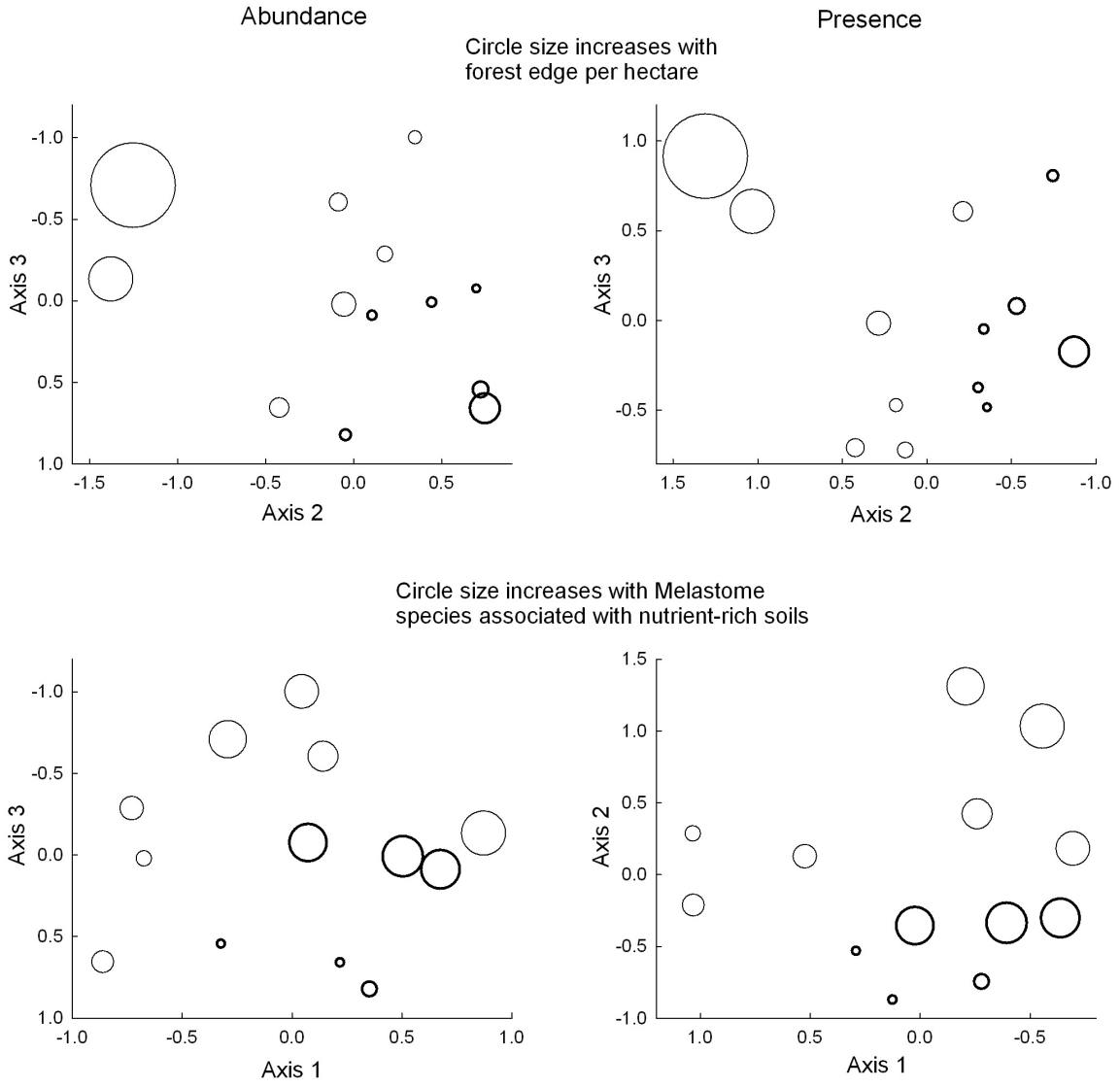

Figure 8.2. Nonmetric multidimensional scaling (NMS) of 13 bird survey sites, using species abundance (left) and presence (right), in all cases using only those 258 wide-ranging species whose range completely overlapped all survey sites. Light and dark circles represent plots north and south of the Amazon River, respectively. In the top graphs, circle size is proportional to mature forest edge per hectare at the 4 km buffer radius, and the x-axis is the NMS axis most strongly correlated with that variable. In the bottom graphs, circle size is proportional to the most important axis of a separate NMS ordination of Melastome plant species composition, and the x-axis is the bird NMS axis most strongly correlated with that Melastome axis. In the ordination of abundance data, axis three was also correlated with Melastome composition, and this was also true for axis two in the ordination of presence data. NMS axis signs are arbitrary, and axes are oriented to show similarities among the graphs.

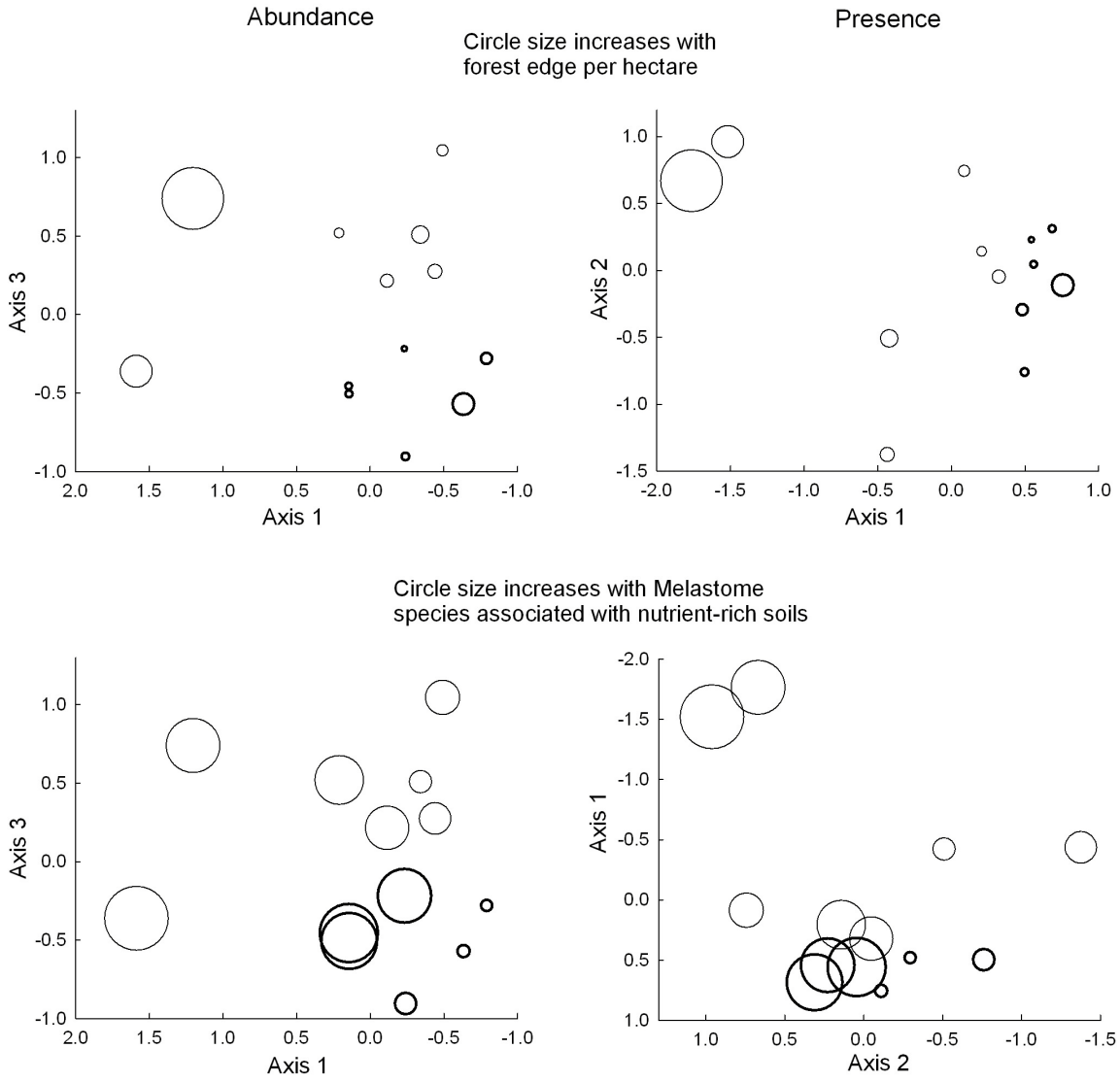

Figure 8.3. Nonmetric multidimensional scaling (NMS) ordinations of 13 bird survey sites, where distance among circle centers is proportional to bird genus compositional difference. Light and dark circles represent plots north and south of the Amazon River, respectively. In the top two plots, the horizontal axis is correlated with forest fragmentation at the 4 km radius, and the vertical axis with the north/south regional distinction (for presence data, axis 1 was correlated with both fragmentation and region). In the bottom plots, the horizontal axis is correlated with Melastome species composition, and the vertical axis with region. Circle size is proportional to the most important axis of an NMS ordination of Melastome species composition. NMS axis signs are arbitrary, and axes are oriented to show similarities among the graphs.

could account for 48 and 47 percent of variability in genus abundance and presence, respectively. Aside from the overall strength of the models, the most striking difference between the species-level and genus-level models was the difference in the relative importance of the three independent variables. Whereas the range map and regional variables dominated the species-level models, the local environmental variables, particularly forest fragmentation, became much more important at the genus level.

Melastome species composition and forest edge per unit area at the 4 km buffer, when included in a multiple regression without range map or regional variables, together accounted for only 15 percent of bird species composition variability ($r^2 = 0.15$, $p<0.02$, abundance data), whereas they accounted for 30 percent of genus variability ($r^2 = 0.30$, $p<0.02$, abundance data). Small tree basal area was not retained in any regression model due to its strong correlation with, but poorer performance than, the fragmentation metrics.

DISCUSSION

Geographic distance and dispersal limitation

The effect of geographic location (distances among sites) was unimportant, and was not retained in regression models at either taxonomic level. The relative locations of the survey sites north or south of the Amazon River were not correlated with distances among sites, so that the important effect of the river as a regional boundary was not simply a distance effect. However, the survey locations relative to species range maps

were correlated with distances among sites, probably due to the much more geographically and taxonomically detailed information that the range maps provide in comparison to the simple regional distinction. This correlation bears upon the question of whether or not dispersal limitation is important in determining beta diversity in Amazonian bird communities, in the following way.

If geographic distance is taken to represent dispersal limitation in a straightforward way, then my findings suggest that dispersal limitation is not important except at the most coarse spatial scales, i.e., the absolute range limits of species. In other words, distances among sites are not useful for explaining beta diversity for those species without range limits between the sites. This is partly reflected in the fact that distance among sites was weakly correlated with bird species abundance differences when all species were included in a Mantel test, but not when only wide-ranging species were included. This could easily have turned out differently, because most species are distributed patchily, with variable abundances within their range limits. My findings suggest that this patchiness, to the extent that it existed among the sites I visited, is better explained by environmental variability than by dispersal limitation. However, at larger spatial scales, dispersal limitation may be important if it is instrumental in determining species range limits. In particular, the Amazon River may represent a dispersal boundary.

Many species and subspecies with limits at the Amazon belong to taxa that are more widely distributed in both regions, with species or subspecies replacements occurring across the river. This pattern strongly suggests that those taxa are derived from basal taxa that were either widely distributed before diversification, or that diversified

along the regional barrier after dispersal across it. Thus, those limits at the river do not suggest endogenous, ecologically neutral dispersal limitation *censu* Hubbell (2001), but they do suggest exogenous limits placed on dispersal by ecological or social conditions. This is also supported by the probability that many species with range limits at the river are capable of crossing the river easily. An example is *Pionites*, a parrot genus with two common, parapatric species separated by the Amazon in the study region. Both species are very strong fliers that can be seen flying long distances over forest canopy, and occasionally over open areas. It is difficult to imagine that endogenous physiological or behavioral traits could have limited their dispersal for a period sufficient for speciation. More likely, one or both species competitively exclude the other through antagonistic social or ecological interactions, or some other aspect of social behavior in the context of different avian communities in the two regions prevents dispersal. On the other hand, the possible role of the very wide river floodplain in physically preventing dispersal over long time periods should not be entirely discounted. There is some evidence that understory bird species show greater genetic disparity across the Amazon River than do canopy species, suggesting that the river has presented a greater physical barrier to weaker dispersers (Burney and Brumfield 2009). Given the large number of species and subspecies with limits at the Amazon, it is certainly possible that different mechanisms have prevented range expansion across the river for different taxa. In either case, the presence of numerous distributional limits in the study region, together with the contrasting lack of correlation between geographic distance and species turnover, suggest

that while dispersal limitation is important for determining beta-diversity at large spatial scales, it is of an ecologically deterministic, rather than neutral, kind.

Species distributions and regional boundaries

Species distributional limits appear to be the most important single factor determining local avian species composition in terra firme forests in Loreto, due primarily to the important regional boundary defined by the Amazon River. This effect was likely at an extreme because I sampled sites north and south of the Amazon, which is arguably the most important bioregional boundary in the Amazon basin for birds. However, distributional limits explained an important component of compositional variability even when species with range limits in the study area were removed from analyses. This was the case mainly because many wide-ranging species exhibited variations in abundance that corresponded geographically to the distributional limits of the range-limited species, particularly but not exclusively at the Amazon River. This effect even remained visible in models for which the dependent matrix was based on presence data; in other words, models that did not include any abundance information. This can be at least partly explained by multiple wide-ranging species that were nonetheless absent from all or most sites on one side of the river, such as *Xiphorhynchus elegans* (see the discussion of this pattern in chapter 6). In these cases, species were often comprised of regionally limited subspecies with distinctive habitat associations.

Local environments

Variations in the edaphic and floristic environmental variables were strongly intercorrelated, Melastome composition generally representing them in the model results. Vegetation structure variables were likewise intercorrelated, and were represented in model results by forest fragmentation at the 4 km buffer width. Both floristic composition and forest fragmentation assumed greater importance than the river and range map variables in the genus and wide-ranging species models, as expected, but those regional variables were nonetheless retained in those models. Results for the wide-ranging species are probably more indicative of the relationship between local environmental variables and range-restricted species than are the all-species results, due to the sampling problem encountered with range-restricted species, as discussed in the preceding chapters. That is, it is likely that floristic and physiognomic habitat associations are just as important for range-restricted as for wide-ranging species.

Regardless, the effect of the Amazon River was more important than any environmental variable in describing overall species turnover among sites. Forest fragmentation in surrounding landscapes was the second most important variable, followed by floristic composition. These results conform to findings in avian biogeography beyond the Amazon Basin, which have suggested that vegetation physiognomy and floristics in particular, and local habitats in general, can strongly influence species distributions, but that spatial variations in habitat characteristics cannot alone account for larger-scale distributional limits.

Regional / local interactions

There were a large number of species whose abundances differed on opposite sides of the Amazon River, and which also comprised subspecies replacements on opposite sides of the river, as discussed in Chapter 6. I also suggest in that discussion that those regional variations in abundance may, in those cases, be due to evolutionarily developed ecological differences between subspecies. Such differences could mean, in other words, that different subspecies have different habitat associations, so that the relatively similar terra firme forests I sampled north and south of the river represent habitats of different quality for the two subspecies. If this is the case, then it is reasonable to consider that some of the habitat associations I examined at the survey site scale may vary regionally, although my sample size was not adequate to test this possibility. Results for at least three species do strongly suggest that floristic associations can vary by region, and in two of those cases (*Myrmotherula menetriesii* and *Tachyphonus surinamus*), there were regional subspecies replacements.

In the case of *M. menetriesii*, a midstory antwren, *M. m. pallida* was common at all sites north of the Amazon, whereas *M. m. menetriesii* was common south of the river only at sites with floristic composition associated with nutrient-rich soils. The species was observed only occasionally on southern sites with nutrient-poor, sandy soils and corresponding floristic composition. When only the six southern sites are considered, the species' relative abundance was significantly associated Melastome composition ($r = 0.75$, $p = 0.04$). Exactly the opposite pattern is suggested by results for *T. surinamus*, a midstory and understory tanager. While *T. s. napensis* was common at all southern sites,

T. s. brevipes was common only at northern sites with floristic composition indicative of nutrient-poor soils. Of the four northern sites with nutrient-rich soil conditions, it was detected on only one, and there it was detected only three times. When only northern sites are considered, relative abundance of *T. surinamus* was associated with Melastome composition ($r = 0.84$, $p = 0.001$). These associations are not likely to have occurred by chance; *M. menetriesii* and *T. surinamus* are both common, widespread species in Loreto, and it is normally difficult to spend days without observing them, if one is in appropriate habitat. The association of *T. surinamus* with sandy-soil forests has been discussed (Hilty and Brown 1986, Schulenberg et al. 2007), but the idea that this association may vary regionally and between subspecies needs further exploration. The possible association of *M. m. menetriesii* with rich-soil forests has, to my knowledge, not been documented.

The third example is *Galbula chalcothorax*, a midstory jacamar typically considered to be strongly associated with várzea forest, and a species that is monotypic within the study region. It occurred as a relatively common species at all three survey sites situated south of the Amazon and on nutrient-rich soils, usually but not exclusively observed at the edges of treefall gaps. It was never observed at southern sites on nutrient-poor soils, and was detected only once at a northern site, again a site on nutrient-rich soils. This species is indeed present in várzea forests widely in the entire region, and is largely absent from terra firme forests north of the Amazon, but apparently occupies nutrient-rich, terra firme forests south of the river. It was nearly significantly correlated with Melastome composition south of the river ($r = 0.84$, $p = 0.10$), but not when all 13 sites were considered.

The small numbers of sites within regions do not offer sufficient power for tests of this kind, but these exploratory results do suggest that habitat associations with specific terra firme forest types may vary regionally, sometimes at the subspecies level. With more within-region sampling, this may eventually be found to be an important form of interaction between local and regional influences on community composition.

Sampling limitations

My study sites were restricted to mature, terra firme forests, and findings are therefore largely limited to that general habitat. For example, bird communities in open agricultural fields in Loreto are very different from those in mature forest, and had that habitat been sampled, local habitat structure (open vs. forest) would almost certainly have been more strongly correlated with species composition than were regional factors such as distributional limits. The same may also be true of the distinction between seasonally inundated (várzea) and upland forest habitats.

The fact that regional associations were stronger at the species level, while local habitat associations were stronger at the genus level (Table 8.1), superficially agrees with the notion that phylogenetic diversity at the species level is of primary importance for bioregional distinctions that mainly describe recent vicariance histories, while niche diversity, which is generally more pronounced at deeper phylogenetic levels, is more important for local habitat associations. However, this is confounded by the sampling problem associated with range-restricted species. Thus, I expect that tests of habitat association that are limited to one region, given the addition of more survey sites, will

show that the number of bird species with strong within-terra firme habitat associations is greater than that demonstrated here. This is supported by the fact that when only wide-ranging species were included in the analyses, species associations with local environmental characteristics were roughly equivalent to those for genera.

Chapter Nine

Conclusions

Biogeography and Conservation of Western Amazonian Birds

The most significant general finding of this study has been that spatial variation in the composition of western Amazonian terra firme bird communities is pronounced, and is very strongly associated with variation in readily identifiable and measurable environmental features at regional, landscape, and local spatial scales. This finding is not surprising, and indeed should appear rather obvious given the large body of research on the spatial components of biological diversity in other regions, particularly in the northern temperate zone. Nonetheless, it stands in contrast to what has until fairly recently been the conventional thinking on Amazonian bird community composition, and on tropical lowland diversity more generally.

There is a substantial literature describing avian distributional limits at major Amazonian rivers and the influence of deforestation patterns on Amazonian bird communities, but their relative and collective contributions to community composition patterns across landscapes have not been measured previously. The additional influence of forest floristics on variation in bird communities has gone practically unstudied in the

Amazon basin. Taken together, these factors bring us a long way toward understanding why Amazonian terra firme bird communities can be so different in different places, despite the superficial similarities of the forests that harbor them.

THE AMAZON RIVER BOUNDARY

Tuomisto (2007) pointed out that spatial discrepancy between present-day environments and taxonomic distributions suggests the lingering influence of historical barriers to dispersal, as opposed to ecological speciation across environmental gradients. Bird distributional disjunctions at the Amazon River appear to be a case of taxonomic disjunction without environmental difference, suggesting vicariant evolutionary histories for a large number of species and subspecies. However, the weight of molecular evidence supports the supposition that most of the speciation events in question are likely to predate the Pleistocene (though this is by no means certain until the necessary genetic studies have been undertaken for the specific taxa in question).

It is also unlikely that the Amazon River itself was the original geographical feature causing vicariance, for several reasons. First, several terra firme bird species that currently have distributional limits at the Amazon do not appear to be physically limited by the river, as discussed in previous chapters. Rather, populations may be behaviorally limited by inhospitable social conditions on the opposite riverbank, whether that entails the presence of a closely related taxon or a more complex suite of interspecific interactions. Competition between sister taxa, of course, cannot have been the driver of a vicariant event that is invoked to explain the divergence of those taxa. Second, only some

species with distributional limits at the Amazon are actually limited by the river along the whole length of their range. Many others have limits along one part of the Amazon but cross it in another; several species included in this study do not cross the Amazon in Loreto, but they do in Brazil. The opposite pattern is even more common—many Amazonian species are limited at the Amazon where it is at its widest in eastern Brazil, but cross it further upstream (Hayes and Sewlal 2004). These patterns suggest that the Amazon has rarely been an absolute physical limit to bird species dispersal, but has commonly been the site of secondary contact after vicariance. Finally, many Amazonian speciation events likely predate the formation of the Amazon itself. The eastern portion of today's Amazon River did not begin draining the western part of the basin until approximately ten million years ago, and the formation of the river's present course took several million additional years (Hoorn 2006a, Figueiredo et al. 2009).

The dramatic changes in Amazonian landscapes that took place during the Miocene and Pliocene will probably be the most productive geological and hydrological phenomena to investigate for potential vicariance events that have contributed to present-day, species-level regional diversity across the Amazon River (and other major rivers in the Amazon Basin). Genetic research points to this time period as important for species diversifications, and Miocene aquatic environments of the western Amazon may have provided abundant opportunity for vicariant isolation of terrestrial taxa. However, there is no reason to suspect that there would have been a strong north-south bias in Miocene vicariance patterns that could explain why so many western Amazonian species are today limited to the northern or southern side of the river (e.g., see maps in Figueiredo et al.

2009). Given this, and the likelihood that many of the species in question predate the formation of the Amazon's current course, it seems clear that post-speciation dispersal has been a critical element influencing modern distributional limits along the river itself. Thus, determining why many species do not, today, disperse across the river may be of greater importance for explaining disjunctions at the Amazon than is the question of where the species originated.

One can alternatively ask whether environmental gradients, rather than vicariant isolation, were important for speciation. Indeed, it seems likely that complex gradients existed among western Amazonian Miocene terrestrial environments. Those gradients, though, must have undergone substantial geographical change since that time, just as in the case of the vicariance model, and so it still seems likely that subsequent dispersal, rather than the specific geography of the original speciation event, would remain the key to understanding modern disjunctions at the Amazon River. This, in turn, should focus attention not only on the Miocene-Pliocene, but also on the Pleistocene as a period when changing surface geomorphology, hydrology, and climate probably drove important changes in the distributions of existing taxa.

All of the environmental data examined in this study suggest that, at the regional spatial scale of this study, today's physical environments are not considerably different in terra firme forests on opposite banks of the upper Amazon, whereas avian communities are substantially different. However, the possibility of environmental difference cannot be ruled out. The range of environmental variables that can potentially be measured is considerable in habitats as complex as those of the Amazon basin, and I only examined a

small handful of variables. Even if environmental conditions on opposite sides of the river are in fact very similar, the notion that environmental similarity with taxonomic difference indicates a vicariant history seems limiting. Environmental gradients change over time, and this together with long periods of dispersal can hypothetically account for modern disjunctions at Amazonian rivers despite present-day environments, just as in the case of vicariance.

The difference between avian and plant community change across the Amazon River is striking. Why should so many distributional limits occur along a river floodplain for animals, but not for plants? The idea that birds are physically dispersal-limited by the floodplain, but plants are not, is unsatisfying, at least as a general rule. In fact, many of the plant species in question depend upon animals for dispersal—many Melastome species considered in this study are dispersed by birds, some of which have distributional limits at the Amazon and some of which do not. The most obvious difference between animals and plants is social behavior: it seems at least possible that social interactions among avian taxa, at the community level wherein species are interacting with a large number of other species, can account for de-facto dispersal limitation across an important geographical feature such as the Amazon floodplain.

LOCAL ENVIRONMENTS

Bird communities in Loreto are clearly influenced by environmental conditions that vary at small to medium spatial scales (that is, within and immediately surrounding the landscape scope defined by the paired one-kilometer transects used in this study). While

some of these effects are well documented for Amazonian birds, others are not, and this study shows that taken collectively, components of forest physiognomy and floristics can account for a large portion of spatial variation in avian community composition.

It is well established that Amazonian bird communities are impacted by forest fragmentation. This study corroborates studies in other Amazonian regions that have associated increased fragmentation of mature forest with reduced species richness, reduced abundances of hunted bird species, and compositional change resulting from both the increased abundance of edge-associated species inside forest and the reduced abundance of forest interior species (Pearman 2002, Barlow et al. 2006, Laurance 2006). Most previous studies have relied on mist-net captures, which only sample birds in the forest understory. Terrestrial, understory, and midstory species did indeed dominate the lists of species in this study whose relative abundances were reduced in the most fragmented forests, but a number of canopy species, both frugivores and insectivores, also appeared to be affected. At the most general level, this might be taken as evidence that patterns detected within a fraction of the avifauna through the use of mist-nets are indicative of patterns in the whole bird community. However, canopy species have been so infrequently studied in this regard that such a conclusion would be premature, and my results might best be taken as foreshadowing interesting and useful results for future studies that focus on canopy species.

The association between forest fragmentation differences and community composition differences became stronger in this study as I considered wider areas around the survey sites, up to the maximum distance I considered (four kilometers). This result

accords with the findings of a similar study in the Ecuadorian Amazon (Pearman 2002), and also accords with general findings in landscape ecology that biological communities can be influenced by landscape composition at considerable distances. Since the ecological mechanisms determining changes in species abundances were not investigated either in this study or by Pearman (2002), a functional explanation of the documented differences and their scale dependencies is not possible, but rather remains an important area for future work. The predictive relationship between fragmentation metrics and community composition differences is in itself useful, though, and the suggestion that fragmentation can strongly influence forest interior bird communities at distances up to, and quite probably exceeding, four kilometers is edifying. Variations in bird communities inside Amazonian forests that appear to be locally quite similar to one another may be explained in some cases by their wider landscape contexts, which may not be at all evident without the aid of satellite imagery, overflights, or intimate local knowledge of surrounding landscapes.

Amazonian terra firme bird community composition is also influenced by the composition of forest plant species: different forest types, defined floristically, have different bird communities. The importance of floristic characteristics in determining avian distribution and abundance, in turn reflecting edaphic effects at least in part, has only recently been recognized at all for Amazonian birds, and this study not only confirms earlier work in this area (Whitney and Alvarez 1998, Isler et al. 2001, Alvarez 2002, Alvarez and Whitney 2003), but further demonstrates that the influences of floristic factors are not limited to just a few specialist species, but are widely important for many

species, so that whole communities are affected in predictable ways. Tropical ecologists and biogeographers wishing to understand spatial patterns of wildlife species occurrence in the Amazonian lowlands must find ways of measuring important floristic variables, despite the discouraging complexity of Amazonian plant communities. Deforestation and forest fragmentation are easy to measure by comparison, but in some ways, floristic variation will be an even more important factor for which to account. For phylogeographers, understanding the role of natural environmental heterogeneity in generating phylogenetic diversity will be critical. For conservation planners, understanding the role of that heterogeneity in maintaining biodiversity in modern landscapes will be of equal importance.

The predominant land cover type in the western Amazon is unfragmented, mature, terra firme forest. It is partly for this reason that the Amazon has historically been thought of as monolithic and uniform. However, a greatly enhanced understanding of the geomorphologic complexity and history of the region has led over the last few decades to the opening of a new window on these forests. They consist of a mosaic of floristic forest types, sometimes grading into one another and sometimes abutting one another abruptly, according in important ways to underlying edaphic patterns. This may be the predominant form of relevant environmental heterogeneity for bird communities across sometimes vast expanses of lowland terra firme forest lacking significant fragmentation. Two of the most striking examples of avian diversity related to edaphic and floristic gradients are described in the next section.

TWO INTERESTING TAXA

Trogon melanurus

Two diagnosable forms of *Trogon melanurus*, a large Trogon (Trogonidae) species, occur in the western Amazon and in other Amazonian regions, but no formal description of the two taxa has yet been made (Bret M. Whitney and José Alvarez Alonso, personal communication, and LYP personal observation). There essentially is a cryptic taxon, *T.* [*melanurus*], within the described *T. melanurus*, probably separable at the species level. The two taxa are readily distinguished in the field on the basis of vocalizations, which are consistent with more subtle plumage differences observable among specimens (Bret M. Whitney personal communication and LYP personal observation). It is not yet clear which taxon will retain the specific epithet *melanurus*, so I use *T.* [*melanurus*] to indicate the fast-vocalization type, which is generally less well known. They are treated in this study as separate species, and a future publication will describe them in detail (Bret M. Whitney, LYP, et al.).

The most interesting questions about *T. melanurus* in the context of this study have to do with the apparent specializations on distinct forest types of the two taxa within the same landscapes. They can occur very closely together where their habitats are adjacent, and their total ranges are widely overlapping (though the extent of this is not currently known). As Figure 9.1 shows, both taxa were observed during the present study, and their patterns of occurrence are closely correlated with forest soil conditions. There are many forest type specialists identified in this study, but this is one of only two taxa (the other being the genus *Herpsilochmus*) in this study's dataset within which very closely related

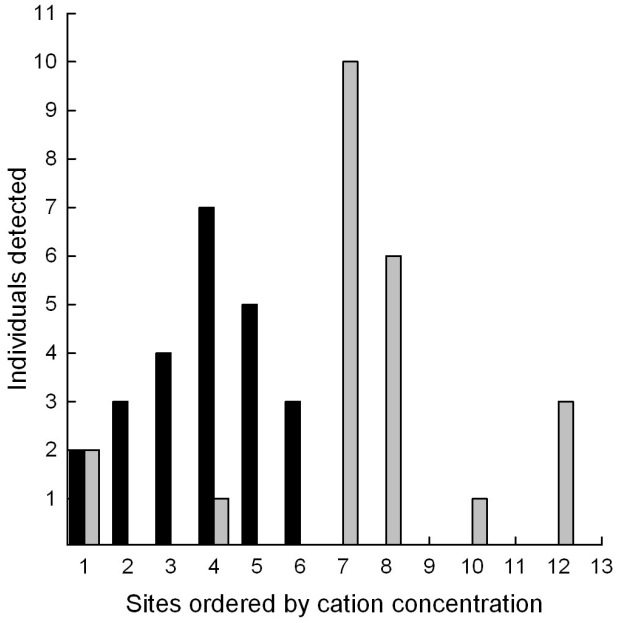

Figure 9.1. Relative abundances of two *Trogon melanurus* taxa at 13 sites in the Peruvian Amazon. Sites are shown in increasing order of summed cation (Na, Ca, K, Mg) concentrations. The fast-song *T.* [*melanurus*], shown with black bars, was detected only at sites with nutrient-poor soils, whereas the slow-song *T. melanurus*, shown with gray bars, was detected predominately at sites with nutrient-rich soils. The two nutrient-poor sites where a few slow-song individuals were detected included some low-lying areas near large streams with várzea-like vegetation, and those individuals were detected in those areas, consistent with other observations of that taxon in várzea habitat outside the study sites. Note also that sites with the highest soil nutrient concentrations seemed to have lower abundances of *T. melanurus* than did sites with intermediate concentrations.

species segregated clearly along an edaphic gradient. Attila *spadiceus* and *A. citriniventris* may represent a third such case, but that example is less clear. The evolution and ecology of these taxa will be particularly important for understanding the role of edaphic heterogeneity in generating and maintaining avian diversity in the western Amazon.

The present-day habitat specializations of the two Trogons bring up the question of whether their speciation has resulted from differential adaptation along an environmental gradient. Of course this hypothesis has to compete with the idea that the modern sympatry of the two taxa has resulted from secondary contact after geographic isolation. Either way, though, habitat specialization would be implicated to some degree in their evolution, because there must have been an evolution of different habitat associations for the two populations in either case.

This relates closely to the question of which of the two species is basal, i.e., more closely related to their next-closest relative (this discussion assumes that the current *T. melanurus* including both taxa is monophyletic, which seems likely but is not certain). If Slaty-tailed Trogon *T. massena* is the basal taxon to both (DaCosta and Klicka 2008), then presumably that question can be answered, independently of hypotheses about which habitat is older, through a genetic comparison of those three taxa. A few other closely related taxa would have to be included in analyses, because there is currently taxonomic confusion within the genus (SACC 2007, DaCosta and Klicka 2008). If the sandy, poor-soil associated *T.* [*melanurus*] turns out to be more closely related to the basal taxon than is the clayey, rich-soil associated *T. melanurus*, then the geologic-historic narrative

outlined by Fine (2005) and Aleixo and Rossetti (2007) may be supported by the evolution of *Trogon*. Those authors have suggested that taxa occupying older geological formations with nutrient-poor soils, chiefly in the eastern Amazon, are often basal to related taxa occupying more recent formations with richer soils in the western Amazon. Aleixo and Rossetti (2007) additionally claimed that some várzea-associated avian taxa appear to have evolved relatively recently in the western Amazon. This might be corroborated if *T. melanurus* is the more derived taxon, since it occupies both nutrient-rich terra firme and várzea floodplains.

On the other hand, Fine (2005) also showed that some plant taxa have evolved specializations to one soil type fairly recently, probably in the presence of both soil types locally, so that speciation is not just tracking geology at the largest spatial and temporal scales, but also responding over short geological time spans to local environmental heterogeneity. Thus, some western Amazonian members of the plant family Bursuraceae that were associated with poor soils were determined to be recently derived from sister taxa on rich soils (Fine et al. 2005). If this may also be the case for birds, then the long-term geological history of South America may not necessarily provide an explanation for the timing and geography of *Trogon* diversification at the species level.

Herpsilochmus

In November 2006, I documented an undescribed form of *Herpsilochmus* antwren at the Nuevo Esperanza site, here tentatively identified as *H. species novum*. Several specimens have since been collected, and the species will be described in an upcoming publication.

The taxon is of particular interest here because it, like the undescribed *T. melanurus* taxon, is almost certainly a specialist occurring only in a particular forest type, associated with nutrient-poor soil conditions.

The genus Herpsilochmus has been in a stage of expansion for the past two decades, both by means of the description of previously unknown species and by the elevation to species status of taxa formerly described at the subspecies level, so that the genus has been expanded from nine to 16 species, and likely will continue to grow as these two activities continue (Whitney et al. 2000). In recent years, the Ash-throated Antwren *H. parkeri* was discovered in a geographically restricted range in the eastern Andean foothills of Peru (Davis and O'neill 1986), and the Ancient Antwren *H. gentryi* was discovered in a specialized habitat type in terra firme forests of the northern Peruvian Amazon (Whitney and Alvarez 1998). Also in recent years, four subspecies in the *H. pileatus* complex have been given species status on the basis of differences in vocalizations and plumages (Davis and O'neill 1986, Whitney et al. 2000).

Herpsilochmus gentryi and *H. sp. novum*, while parapatric and range-restricted, are both sympatric with the more widely distributed *H. dugandi*, itself recently elevated to species status within the *H. sticturus* superspecies (Ridgely and Tudor 1994, Zimmer and Isler 2003). Both *H. gentryi* and *H. sp. novum* are specialists of forests growing on nutrient poor, terra firme soils, while *H. dugandi* appears to occur only in várzea floodplain forests and in terra firme forests over nutrient-rich soils, so that there appears to be little or no overlap in local habitat occupancy between the species. This is true despite the fact that both *H. gentryi* and *H. sp. novum* can be found within hearing

distance of *H. dugandi* where the appropriate habitats adjoin. None of these three species are likely sister taxa despite their geographic proximity, *H. dugandi* being considered allied with *H. sticturus* (Zimmer and Isler 2003), and *H. gentryi* with Todd's Antwren *H. stictocephalus* (Whitney and Alvarez 1998). Thus, their modern sympatry has likely resulted from significant range shifts, which in turn are likely to have resulted from complex historical geomorphologic processes.

As has been the case for an increasing number of newly discovered species, *H. species novum* was initially recognized by its distinctive primary vocalization, or loudsong, which immediately recalled a *Herpsilochmus* antwren when I first heard it, despite its strong distinctiveness within the group. While playback of the loudsong and subsequent visual observation confirmed the initial generic identification, it appeared visually indistinguishable from *H. dugandi*, which occurs in the region. Neither could it be visually distinguished from *H. dorsimaculatus*, with which it is not currently known to be sympatric, but which occurs nearby, east of the Putumayo River in Columbia. This problem is typical of the genus—males of most species are visually indistinguishable in the field. Despite visual similarities, the loudsong was unlike either of those species, or indeed any member of the genus. Thus, as in several other recent cases, the discovery of this taxon illuminates the critical importance of vocalizations in both the detection of undescribed taxa and the taxonomic classification of birds, a point that has been stressed by several authors (Isler et al. 1998, Peterson 1998).

Herpsilochmus sp. novum has been observed and recorded in two distinctive habitats, representing two distinct forms of terra firme forest growing on sandy, nutrient-

poor soils. The type specimen was collected in relatively short stature forest on nutrient-poor soils found principally adjacent to the Amazon River floodplain. This forest type occurs on extremely flat terra firme terrain that may have at one time comprised portions of the floodplain itself. Soils are generally a poorly drained mixture of light-colored clay and sand. The species has also been documented in upland forests further north from the Amazon River, in tall forests on nutrient-poor soils east of the Napo River (Haven Wiley, personal communication and audio recordings). These forests grow on much more deeply incised, hilly terrain at slightly higher elevations, where soils contain more sand and understory stands of *Irapay* (*Lepidocaryum tenue*) palm are common.

Both of these forest types are distinct from the *varillales*, or white sand forests, where *H. gentryi* is common within its range. Neither forest type is as short-statured as a typical varillal, nor are soils as sandy and nutrient-poor. However, *H. gentryi* also occurs more widely in tall forests on sandy-hilly terrain that is extremely similar to those in which *H. sp. novum* has been found to the east of the Napo; in particular, *H. gentryi* occurs in forests on the Nauta formation (Räsänen et al. 1998, Whitney and Alvarez 1998, Rebata et al. 2006). Thus, the two species appear to occupy very similar habitats parapatrically, with range limits somewhere near the Napo River, while each species also occupies an additional, distinctive habitat within its own range.

Near the Yaguasyacu River, Satellite imagery and digital elevation models clearly show abrupt transitions from the topographically flat areas near the Amazon River floodplain to very hilly areas to the north, suggesting geologically recent fluvial activity as a principle determinant of the difference between the two habitats. We have confirmed

that *H. dugandi* occurs in the clayey-hilly forests, as well as in the várzea forests near the Amazon River, where these habitats have been locally sampled. To the west of the Yaguasyacu River, on the upper Apayacu River, hilly terrain similarly replaces flat terra firme terrain as one moves north from the Amazon River floodplain, but here, the hilly terrain is constituted of the very sandy, nutrient-poor soils referred to above. Where this habitat has been sampled, it has been found to contain *H. species novum* (H. Wiley, personal communication and audio recordings). Thus, the species appears generally to occupy poor-soil, terra firme forests east of the Napo River and north of the Amazon River, where *H. dugandi* occupies adjacent, rich-soil terra firme and várzea forests. Whether or not the overall distributional limits of *H. species novum* are concordant with the rivers is entirely unknown.

Conservation status within Herpsilochmus antwrens is associated with range size—those species considered threatened have very restricted distributions, within which they are associated with habitats that are being converted for agricultural and other economic uses. The Pectoral Antwren *H. pectoralis* is an IUCN Vulnerable species occupying gallery forest, deciduous woodland, and tall caatinga in a limited range in northeastern Brazil, and the Ash-throated Antwren *H. parkeri* is an IUCN Threatened species occupying a tiny range in Peru's Andean foothills where agricultural expansion, e.g. for coca and coffee production, is rapidly removing forest habitats. Of the 16 Herpsilochmus species currently described, only those two have formal IUCN status, while *H. gentryi* is considered near-threatened. While common within its very small range, *H. gentryi* may eventually become threatened by agricultural expansion as

populations increase in the region, particularly along the Iquitos-Nauta highway, which bisects the southeastern end of the species' range.

Herpsilochmus sp. novum may be similarly categorized as near-threatened by virtue of range restriction; it appears to occur at high densities within appropriate habitat, and there appears to be no imminent threat of rapid forest loss in the region. Furthermore, nearly all of the locations from which the species is currently known are mature forest tracts actively used by local communities for extractive activities including small-scale timber harvest. It has not, however, been found to occur in nearby secondary forest, whereas it certainly occurs in primary forest interior further from local villages, where extractive activities are more limited.

While extensive forest loss in the region would certainly threaten the species, there may be reason to believe that such loss is not to be expected, at least in the near term. The Ampiyacu-Apayacu region is currently the focus of conservation planning efforts by several groups, importantly including Loreto's regional government. After the recently designated Tamshiyacu-Tahuayo Communal Reserve south of the Amazon River near Iquitos, the Ampiyacu-Apayacu is planned as the second communal reserve in a series of conservation areas planned in Loreto, with legal protection at the provincial level. If designated, this reserve would contain most of the currently known range of the species, although the true range is likely much larger. Due to the species' apparent tolerance of limited forest extractive activities, the Communal Reserve level of protection may be adequate for maintaining healthy populations.

CONSERVATION

Successful conservation planning depends in part on the accurate identification of taxonomically complimentary, or distinctive, areas, so that the full array of taxa in a given region can be included inside conservation areas. Because the taxa of interest can rarely be surveyed in all areas of interest, more easily assessed surrogates, such as gross vegetation features, regional boundaries, and climatic variables, are potentially useful for prioritizing areas for conservation attention. Some of the variables shown here to be strongly correlated with bird taxa turnover, then, are potentially important in this regard. Proxies for the important explanatory factors identified here are extractable from satellite imagery, and it may be possible to partially predict community distinctiveness across wide areas in the Amazon with a combination of image analysis and rapid field surveys.

However, the situation in the Iquitos region with regard to local deforestation and the location of the Amazon River is somewhat idiosyncratic, and may make these factors appear more important than they generally are in other Amazonian regions. While forest fragmentation metrics may be important where fragmentation exists, much of the western Amazon basin still exists as relatively unfragmented expanses of forest, by comparison to the area I sampled. In particular, fragmentation decreases as one moves away from large rivers. Fragmentation effects and other anthropogenic factors are clearly important for conservation planning at medium landscape scales, and in particular, their interactions with underlying patterns of biogeographic heterogeneity are of interest. They will likely be of less interest, though, in complementarity analyses at larger spatial scales in the western Amazon, for which the chief objective is to map natural biogeographic diversity.

By the same token, forest fragmentation is much more widespread in some Amazonian regions, particularly in parts of the Brazilian Amazonian, and conservation planning obviously must take deforestation and fragmentation effects into account in places where they are sufficiently widespread to take on significant regional pattern.

The Iquitos region is also idiosyncratic due to the importance of the Amazon River as a biogeographic boundary. Its biogeographic influence is probably unmatched by any other river, although there are other major rivers in the Brazilian Amazon with known bioregional significance such as the Rio Negro and Rio Madeira. Smaller rivers in the western Amazon such as the Juruá have been found to be unimportant to the biogeography of at least some taxa (Patton and da Silva 2005), and my findings for the Amazon should not be interpreted as necessarily representative of either smaller rivers in the western Amazon or of non-avian taxa. While rivers of intermediate size such as the Napo and the Pastaza may be found to be of some importance for delineating biogeographic regions, the required studies largely remain to be undertaken. Currently recognized distributional limits of avian taxa do suggest that at least the Napo may be of some importance in Loreto, though significantly less than the Amazon itself.

The importance of major Amazonian rivers as boundaries of distinctive avian biogeographic regions, as attested in the case of the Amazon River in Loreto, is clear, and this must be taken into account in conservation planning at the largest spatial scales. It should be noted that this is true regardless of the historical causes of the biogeographic differentiation of regions. Efforts to introduce complementarity into conservation planning may appear suspect when the theory of biogeographic differentiation is itself

suspect. What matters in the end, though, is not the correctness of the theory, but whether the complementarity assessment that it produces actually maximizes complementarity (Schulman et al. 2007). In the specific case of the Pleistocene refugia debate, a closer look may be warranted. In that case, the biogeographic regions in question were mainly derived from avian species distributions. That approach was probably inadvisable as a method of inferring vicariance histories. However, because it used similar data to what today might be used for a complementarity analysis (with important refinements of range maps according to improved knowledge of distributional limits in recent years), the resulting regions are probably relevant for conservation planning, even if the Pleistocene refugia theory is entirely incorrect. The critical caveat is that a conservation plan outlined regionally, using only avian distribution data, should not be presumed to produce an effective complementarity assessment for any taxa besides birds.

This study suggests that the Amazonian regions delineated according to avian distributions may be of little importance for plants. They may be relevant for some other taxa, particularly mammals, but this has not been systematically tested. Perhaps of even greater importance for conservation planning, I was not able to identify any environmental variables capable of even partly explaining the regional difference across the Amazon River. Complementarity studies have become increasingly focused on physical-geographic environmental variables as surrogates for biodiversity, due to the generality of congruence between their spatial distributions and those of a wide array of biological taxa. However, they may not be useful at large spatial scales if large-scale biogeographic heterogeneity occurs in the absence of important environmental

heterogeneity, which may be the case for some components of Amazonian biodiversity. There is also the very credible possibility that there are in fact important forms of environmental heterogeneity that have not been accounted for, but that could explain observed biogeographic heterogeneity. In terms of conservation planning, though, this is not of great relevance, because if the salient environmental variables cannot be identified, then they obviously cannot be used as surrogates.

The forest structure and floristic variables shown here to be strongly correlated with components of bird taxa turnover should also be considered potentially important for conservation planning. Luckily, there are tractable ways of accounting for Amazonian forest type variability. Efficient floristic survey methods have been developed, and improvements will doubtless continue to be made in this regard. Floristic surveys have shown that forest type variation is visible in satellite imagery, and an important research direction will be to assess the predictive ability of satellite imagery for wildlife species distributions and community composition. For the reasons discussed above, this approach is likely to be of great utility within, but not across, the largest avian biogeographic units within the Amazon basin.

Surrogacy relationships between plants and birds may thus be scale dependant. I have studied relationships between the two groups within only a small area, across only one major biogeographic boundary, so this conclusion is very tentative. However, it may eventually be found to be generally true across the Amazon basin that while floristic variation within regions can predict important components of avian community variation, additional distinctions that are not apparent in floristic datasets at larger scales are

necessary to define avian community variation among Amazonian regions. At the same time, there may be continental-scale floristic heterogeneity (e.g., ter Steege et al. 2006) that is associated in important respects with avian species turnover, even if those patterns are not concordant with river-bounded regions or other regional designations.

Conservation planning based on niche modeling for individual species is also affected by the notion that avian distributional limits cannot always be predicted from environmental variables. Most environmental variables for which sufficient datasets exist today to develop spatially explicit niche models for Amazonian species do not show significant variation across the Amazon River, or across other major rivers in the Amazon basin. Accordingly, avian niche models produce distributions that cross the river, even for species that are known to be limited at the river (LYP unpublished data). More generally, niche modeling for Amazonian bird species is likely to over-predict actual distributions, and models will be more accurate if they are only taken to be valid within the known distributions of species (the realized niche). This problem undoubtedly results partly from the insufficiency of currently available environmental data, but it also results from real distributional limits that may not be modeled with even the best environmental datasets. On the other hand, this cautionary recommendation is by no means intended to discourage efforts to expand and improve the known distributions of species via a combination of careful niche modeling and collection of ground truth data.

WESTERN AMAZONIAN BIRD COMMUNITY COMPOSITION

Bird species and genus composition varied strongly among sites, and variation was closely correlated with variation in plant species composition (driven to a large extent by soil type), human disturbance associated with forest fragmentation, and survey site position north or south of the Amazon River. By far the strongest differences in bird species composition were between forests on opposite sides of the Amazon River, despite the fact that local environments were not different on opposite sides of the river. This strongly suggests that historical biogeographic factors, rather than present-day environmental gradients, are responsible for bioregional boundaries at Amazonian rivers. Locally, forest fragmentation was more strongly correlated with bird species and genus composition than was floristic variation, even though fragmentation levels were low relative those seen in some other Amazonian regions. This confirms the strong influence that anthropogenic habitat fragmentation has on forest animal communities, including reductions in species richness. Floristic variation accounted for a third component of avian community variation, and this is of particular importance because it represents the primary form of forest heterogeneity across large expanses of unfragmented western Amazonian regions.

The importance that has previously been attributed to the Amazon River as a bioregional boundary for birds was confirmed both within and among species and genera, and broadly across bird groups that varied ecologically and taxonomically. However, this bioregional boundary for birds may not be present for other taxa. In particular, plant species composition at the species level did not vary systematically between regions

north and south of the river. This underscores the pressing need to re-evaluate general notions of bioregional complexity and pattern in the Amazon basin. The role of edaphic, and by extension forest type, heterogeneity in structuring Amazonian bird diversity has previously been given far less attention than river boundaries and forest fragmentation. The results of this study demonstrate that understanding the historical development and present-day spatial specificities of Amazonian soils and vegetation will be critical for explaining avian diversity and distributions in the region.

These findings significantly advance our understanding of the dimensions and spatial specificities of avian diversity in the western Amazon, but in a sense they only open a door to a large body of work that remains to be done. Several important relationships, such as those between bird communities and insect communities, and between bird communities and climate, have hardly been examined in the Amazon basin. The ecological and physiological mechanisms underlying avian specializations on floristically distinctive Amazonian forest types may be related to evolved tolerances for the defensive compounds found in tree leaves, and possibly passed to insect predators, but this has not been investigated. Coarsely described differences between eastern and western Amazonian bird communities may be partly explained by the geomorphologic, and resulting floristic, associations demonstrated in this dissertation at a more local spatial scale; investigating this possibility will require more spatially extensive sampling.

Climate change will be important for the future of Amazonian bird community distributions, and long-term studies of temporal community change should include avian monitoring. There is evidence that elevated levels of carbon dioxide are accelerating tree

growth rates across the Amazon basin (Phillips et al. 1998, Lewis et al. 2004), an effect which appears to be global in scope (Lewis et al. 2009). At the same time, the region is generally expected to become drier. Increased drought severity can reverse biomass gains by killing trees and possibly alter species compositions as a result of species-specific drought tolerances (Phillips et al. 2009). It is certainly possible that changes in floristics, avian food productivity, and habitat structure will be of sufficient magnitudes to influence bird population densities and distributions.

The finding that many widely distributed species with systematic abundance differences across the Amazon River comprise subspecies pairs raises questions about taxonomic, genetic, and ecological diversity. Most subspecific distinctions in the literature are based on morphological difference, whereas it has been increasingly recognized that morphological and genetic difference are not always concordant. As many as half of morphologically described tropical avian subspecies may not be genetically monophyletic (Phillimore and Owens 2006). At the same time, there is evidence for important genetic disparity within species across the upper Amazon River (Burney and Brumfield 2009). Focused studies of particular species will shed more light on questions of genetic and morphological co-variation, and ecological difference may be a good guide for choosing study species. For example, while nearly half of all the species in this study that showed abundance variation across the Amazon River comprised subspecies pairs on opposite banks, the other half showed abundance variation across the river without any described taxonomic variation (no subspecific disjunction). Those species may be considered important candidates for museum collection and phylogenetic

investigation, because they could harbor cryptic genetic and taxonomic diversity. Alternatively, it may be found that the geographic concordance between morphology and ecology described here is not reflected in genetic disparity. Questions of this kind should guide new avenues for research that investigate linkages among various components of lowland tropical forest biodiversity, their physical and social environments, their histories, and possibly their futures.

Appendix 1. The following 334 bird species were detected during transect surveys and included in analyses. **Region**: (Note 1) Species restricted to one region, north (N) or south (S) of the Amazon River in the study area, but whose distributional limit may or may not be specifically at the Amazon. **Amazon**: Species with distributional limits specifically at the Amazon River in the study region, as defined in Schulenberg et al. (2006). **Subspecies limits at Amazon**: In cases where species comprised at least two subspecies, with the disjunction between them occurring at the Amazon, the northern (N) and southern (S) subspecies are indicated. The sources used to determine subspecies limits are given in the text. The final four columns indicate results of indicator species analyses, as described in the text, showing only significant results at the $p < 0.05$ level. **River**: (Note 2) Significantly associated with a region north (N) or south (S) of the Amazon. **Mel**: Significantly associated with Melastomataceae species compositions indicative of nutrient-poor soils (P) or nutrient-rich soils (R). **Frag**: Significantly associated with low (L) or high (H) forest fragmentation in landscapes surrounding the survey transects, as indicated by the forest edge-to-area ratio within 4 km of transects. **Basal**: Significantly associated with low (L) or high (H) basal area of small (<10 cm DBH) woody stems at survey sites, where low basal area is often indicative of a more open understory and midstory.

Family, *Species*	Region	Amazon	Subspecies limits at Amazon	River	Mel	Frag	Basal
Tinamidae							
Tinamus major							
Tinamus guttatus				S		L	
Crypturellus cinereus							
Crypturellus soui			N *nigriceps*; S *inconspicuus*				
Crypturellus obsoletus	Note 3						
Crypturellus strigulosus	S						
Crypturellus variegatus							
Cracidae							
Penelope jacquacu							
Ortalis guttatus							
Nothocrax urumutum	N	Y					
Odontophoridae							
Odontophorus gujanensis			N *buckleyi*; S *rufogularis*				
Odontophorus stellatus	S	Y		S			
Ardeidae							
Tigrisoma lineatum							
Agamia agami							
Zebrilis undulatus							

Family, *Species*	Region	Amazon	Subspecies limits at Amazon	River	Mel	Frag	Basal
Cathartidae							
Cathartes aura							
Sarcoramphus papa							
Accipitridae							
Leptodon cayanensis							
Harpagus bidentatus							
Leucopternis melanops	Note 4						
Leucopternis kuhli	S						
Leucopternis semiplumbeus	Note 5						
Buteogallus urubitinga							
Buteo magnirostris						H	
Morphnus guianensis							
Harpia harpyja							
Spizaetus tyrannus							
Spizaetus ornatus							
Falconidae							
Herpetotheres cachinnans							
Micrastur ruficollis							
Micrastur gilvicollis							
Micrastur mirandollei							
Micrastur semitorquatus							
Ibycter americanus				S		L	
Daptrius ater							
Falco rufigularis							
Psophiidae							
Psophia crepitans	N	Y					
Psophia leucoptera	S	Y					
Columbidae							
Patagioenas plumbea							
Patagioenas subvinacea							
Leptotila rufaxilla							
Geotrygon sapphirina							
Geotrygon montana							

Family, *Species*	Region	Amazon	Subspecies limits at Amazon	River	Mel	Frag	Basal
Psittacidae							
Ara ararauna							
Orthopsittaca manilata							
Aratinga leucophthalma							
Aratinga weddellii							
Pyrrhura picta	S; Note 6	Y		S			
Pyrrhura melanura	N	Y		N			
Forpus sclateri							
Brotogeris cyanoptera							
Touit huetii							
Touit purpuratus							
Pionites melanocephalus	N	Y		N		H	
Pionites leucogaster	S	Y		S			
Gypopsitta barrabandi							
Pionus menstruus							
Amazona ochrocephala							
Amazona farinosa				S		L	
Cuculidae							
Piaya cayana							
Piaya melanogaster							L
Neomorphus pucheranii			N *pucheranii*; S *lepidophanes*				
Strigidae							
Megascops watsonii			N *watsonii*; S *usta*				
Pulsatrix perspicillata							
Glaucidium brazilianum							
Caprimulgidae							
Nyctidromus albicollis							
Trochilidae							
Topaza pyra							
Florisuga mellivora							
Glaucis hirsutus							
Threnetes leucurus							
Phaethornis atrimentalis							

Family, *Species*	Region	Amazon	Subspecies limits at Amazon	River	Mel	Frag	Basal
Trochilidae							
Phaethornis ruber							
Phaethornis hispidus							
Phaethornis philippii	S	Y		S			
Phaethornis bourcieri	Note 7			N			
Phaethornis malaris			N *moorei*; S *ochraceiventris*			H	
Heliothryx auritus							
Heliodoxa schreibersii	N	Note 8					
Heliodoxa aurescens							
Chlorostilbon notata							
Thalurania furcata							
Trogonidae							
Pharomachrus pavoninus							
Trogon viridis							
Trogon curucui							
Trogon violaceous							
Trogon rufus							
Trogon melanurus	Note 9						
Trogon [*melanurus*]	Note 9				P		
Alcedinidae							
Chloroceryle aenea							
Momotidae							
Electron platyrhynchum							
Baryphthengus martii							
Momotus momota							
Galbulidae							
Galbula albirostris	N	Y		N			
Galbula cyanicollis	S	Y		S			
Galbula chalcothorax							
Galbula dea				S	P		
Jacamerops aureus							

Family, *Species*	Region	Amazon	Subspecies limits at Amazon	River	Mel	Frag	Basal
Bucconidae							
Notharchus hyperrhynchus							
Notharchus ordii					P		
Notharchus tectus							
Bucco macrodactylus							
Bucco tamatia							
Bucco capensis							
Nystalus striolatus	S	Y					
Malacoptila fusca	N	Y					
Malacoptila rufa							
Micromonacha lanceolata							
Nonnula rubecula							
Nonnula brunnea	N	Y					
Nonnula ruficapilla			N *rufipectus*; S *ruficapilla*				
Monasa morphoeus							
Chelidoptera tenebrosa							
Capitonidae							
Capito auratus			N *auratus*; S *insperatus /orosae*	N	R		
Eubucco richardsoni			N *richardsonii / nigriceps*; S *aurantiicollis*		R		
Ramphastidae							
Ramphastos tucanus							
Ramphastos vitellinus					R		
Selenidera reinwardtii			N *reinwardtii*; S *langsdorffii*				
Pteroglossus inscriptus							
Pteroglossus azara			N *azara*; S *mariae*				
Pteroglossus castanotis							
Pteroglossus pluricinctus	N	Y		N			
Pteroglossus beauharnaesii	S	Y		S			
Picidae							
Picumnus aurifrons	S	Y					
Melanerpes cruentatus							
Veniliornis affinis							
Piculus flavigula							

Family, *Species*	Region	Amazon	Subspecies limits at Amazon	River	Mel	Frag	Basal
Picidae							
Piculus chrysochloros							
Celeus grammicus							
Celeus elegans				N			
Celeus flavus							
Celeus torquatus							
Dryocopus lineatus							
Campephilus rubricollis							
Campephilus melanoleucos					R		
Furnaridae							
Sclerurus mexicanus							
Sclerurus caudacutus							
Synallaxis rutilans			N *caquetensis*; S *amazonica*				
Berlepschia rikeri							
Ancistrops strigilatus							
Hyloctistes subulatus							
Philydor erythrocercum			N *subfulvum*; S *lyra*				
Philydor erythropterum							
Philydor pyrrhodes				S		L	
Automolus ochrolaemus			N *turdinus*; S *ochrolaemus*				
Automolus infuscatus							
Automolus rubiginosus							
Xenops milleri					P		
Xenops minutus							
Dendrocincla fuliginosa				N			
Dendrocincla merula							
Deconychura longicauda			N *connectens*; S *pallida*				
Deconychura stictolaema							
Sittasomus griseicapillus							
Glyphorynchus spirurus							
Nasica longirostris							
Dendrexetastes rufigula							
Xiphocolaptes promeropirhynchus							

Family, *Species*	Region	Amazon	Subspecies limits at Amazon	River	Mel	Frag	Basal
Furnaridae							
Dendrocolaptes certhia			N *radiolatus*; S *juruanus*				
Dendrocolaptes picumnus							
Xiphorhynchus ocellatus			N *napensis*; S *perplexus*	N			
Xiphorhynchus elegans			N *ornatus*; S *juruanus*	S			
Xiphorhynchus guttatus					R		
Lepidocolaptes albolineatus							
Campylorhamphus procurvoides	N	Y					
Thamnophilidae							
Cymbilaimus lineatus							
Frederickena unduligera			N *fulva*; S *diversa*				
Thamnophilus schistaceus			N *capitalis*; S *dubius*				
Thamnophilus murinus							
Thamnophilus aethiops	S	Y		S			
Megastictus margaritatus	N	Y		N		H	
Thamnomanes ardesiacus	N	Y		N			
Thamnomanes saturninus	S	Y		S			
Thamnomanes caesius	N	Y		N			
Thamnomanes schistogynus	S	Y					
Pygiptila stellaris							
Epinecrophylla haematonota			N *pyrrhonota*; S *haematonota*	S			
Myrmotherula brachyura				S			
Myrmotherula ignota							
Myrmotherula sclateri	S	Y		S			
Myrmotherula hauxwelli			N *suffusa*; S *hauxwelli*	N			
Myrmotherula axillaris				S			
Myrmotherula longipennis			N *longipennis / zimmeri*; S *garbei*				
Myrmotherula menetriesii			N *pallida*; S *menetriesii*				
Dichrozona cincta							
Herpsilochmus dugandi	N	Y					
Herpsilochmus gentryi	N						
Herpsilochmus species novum	Note 10						
Microrhopias quixensis			N *quixensis*; S *intercedens*				

Family, *Species*	Region	Amazon	Subspecies limits at Amazon	River	Mel	Frag	Basal
Thamnophilidae							
Hypocnemis peruviana			N *saturata*; S *peruviana*				
Hypocnemis hypoxantha					P		L
Terenura humeralis						L	
Cercomacra cinerascens			N *cinerascens*; S *sclateri*	S			
Cercomacra serva			N *serva*; S *hypomelaena*	S			
Myrmoborus myotherinus			N *elegans*; S *myotherinus*	S			
Sclateria naevia							
Percnostola rufifrons	N						
Percnostola arenarum	N						
Schistocichla schistacea						L	
Schistocichla leucostigma						H	
Myrmeciza hemimelaena	S	Y		S			
Myrmeciza castanea	N	Y					
Myrmeciza fortis							
Pithys albifrons	N	Y					
Gymnopithys leucaspis	N	Y		N			
Gymnopithys salvini	S	Y		S			
Rhegmatorhina melanosticta			N *melanosticta*; S *purusiana*		R		
Hylophylax naevius				S			
Dichropogon poecilinota			N *lepidonota*; S *gutturalis*			L	
Phlegopsis erythroptera			N *erythroptera*; S *ustulata*				
Formicaridae							
Formicarius colma							
Formicarius analis			N *zamorae*; S *analis*				
Chamaeza nobilis			N *rubida*; S *nobilis*				
Grallariidae							
Grallaria dignissima	N	Y					
Myrmothera campanisona			N *signata*; S *minor*			L	
Conopophagidae							
Conopophaga aurita			N *occidentalis*; S *australis*				
Conopophaga peruviana							

Family, *Species*	Region	Amazon	Subspecies limits at Amazon	River	Mel	Frag	Basal
Rhinocryptidae							
Liosceles thoracicus							
Tyrannidae							
Tyrannulus elatus							
Myiopagis gaimardii							
Myiopagis caniceps							
Ornithion inerme							
Phaeomyias murina							
Corythopis torquata							
Zimmerius gracilipes							H
Mionectes oleagineus							
Myiornis ecaudatus							
Lophotriccus vitiosus			N *affinis*; S *congener*	S			
Hemitriccus minimus				S			
Poecilotriccus capitalis	N	Y					
Todirostrum chrysocrotaphum			N *guttatum* / *chrysocrotaphum*; S *neglectum*				
Cnipodectes subbrunneus							
Rhynchocyclus olivaceus							
Tolmomyias assimilis							
Tolmomyias poliocephalus					R		
Tolmomyias flaviventris							
Onychorhynchus coronatus							
Myiobius barbatus			N *barbatus*; S *amazonicus*				
Terenotriccus erythrurus			N *signatus*; S *brunneifrons*				L
Neopipo cinnamomea					P		
Legatus leucophaius				S		L	
Myiozetetes luteiventris							
Pitangus sulphuratus							
Conopias parvus							
Megarynchus pitangua							
Tyrannopsis sulphurea							
Tyrannus melancholicus							
Rhytipterna simplex							

Family, *Species*	Region	Amazon	Subspecies limits at Amazon	River	Mel	Frag	Basal
Tyrannidae							
Ramphotrigon ruficauda					P		
Attila citriniventris				S			
Attila bolivianus	S	Y					
Attila spadiceus					R		
Cotingidae							
Phoenicircus nigricollis	N	Y		N			
Cotinga maynana							
Cotinga cayana							
Lipaugus vociferans							L
Gymnoderus foetidus							
Querula purpurata							
Pipridae							
Neopelma chrysocephalum	N						
Tyranneutes stolzmanni							
Machaeropterus regulus							L
Lepidothrix coronata			N *carbonata*; S *coronota*				
Manacus manacus			N *interior*; S *expectatus*				
Chiroxiphia pareola			N *napensis*; S *regina*		R		
Heterocercus aurantiivertex	N; Note 11	Y					
Dixiphia pipra			N *coracina* / *discolor*; S *microlopha*		P		
Pipra erythrocephala	N	Y		N			
Pipra rubrocapilla	S	Y		S			
Piprites chloris							
Tityridae							
Tityra semifasciata							
Schiffornis turdinus					P		
Laniocera hypopyrra							
Iodopleura isabellae							
Pachyramphus marginatus							
Pachyramphus minor							

Family, *Species*	Region	Amazon	Subspecies limits at Amazon	River	Mel	Frag	Basal
Vireonidae							
Cyclarhis gujanensis							
Vireolanius leucotis							
Hylophilus thoracicus							
Hylophilus hypoxanthus							
Hylophilus ochraceiceps							
Corvidae							
Cyanocorax violaceus							
Troglodytidae							
Microcerculus marginatus			N *marginatus*; S *bolivianus* ?; Note 12	N			
Campylorhynchus turdinus							
Thryothorus coraya	N	Y		N			
Thryothorus genibarbis	S	Y		S			
Cyphorhinus arada							
Polioptilidae							
Microbates collaris	N	Y					
Microbates cinereiventris	N						
Ramphocaenus melanurus			N *badius*; S *amazonum*	S			
Polioptila clementsi	N						
Turdidae							
Turdus lawrencii							
Turdus albicollis							
Thraupidae							
Paroaria gularis							
Tachyphonus cristatus	N	Y		N		H	
Tachyphonus rufiventer	S	Y		S			
Tachyphonus surinamus			N *brevipes*; S *napensis*	S			
Lanio fulvus	N	Y					
Lanio versicolor	S	Y		S			
Thraupis palmarum							
Tangara xanthogastra							
Tangara mexicana							
Tangara chilensis							

Family, *Species*	Region	Amazon	Subspecies limits at Amazon	River	Mel	Frag	Basal
Thraupidae							
Tangara velia							
Tangara callophrys				N			
Tangara gyrola							
Tangara schrankii					R		
Tersina viridis							
Dacnis albiventris							
Dacnis lineata							
Dacnis flaviventer							
Dacnis cayana							
Cyanerpes nitidus					P		
Cyanerpes caeruleus							
Cyanerpes cyaneus							
Chlorophanes spiza							
Hemithraupis flavicollis			N *peruana*; S *sororia*				H
Habia rubica							
Cardinalidae							
Saltator grossus							L
Saltator maximus							
Cyanocompsa cyanoides				S		L	
Parulidae							
Phaeothlypis fulvicauda							
Icteridae							
Psarocolius angustifrons							
Psarocolius viridis							
Psarocolius decumanus			N *decumanus*; S *maculosus*		R		
Psarocolius bifasciatus							
Clypicterus oseryi					R		
Ocyalis latirostris							
Cacicus cela							
Cacicus haemorrhous					R		
Icterus cayanensis			N *chrysocephalus*; S *cayanensis*				

Family, *Species*	Region	Amazon	Subspecies limits at Amazon	River	Mel	Frag	Basal
Fringillidae							
Euphonia laniirostris							
Euphonia chrysopasta							
Euphonia minuta							
Euphonia xanthogaster				S		L	
Euphonia rufiventris				S			

See Appendix 1 notes on following page.

Appendix 1 Notes.

1. The Region column indicates species that are only known to occur on one side of the Amazon River *in the study area*, i.e., from the beginning of the Amazon River at the confluence of the Marañon and Ucayali Rivers near the town of Nauta, downstream to the town of Pebas, near the Brazilian border. Some of those species do cross the Marañon or Ucayali further west and south, or cross the Amazon further east in Brazil. The species that are indicated throughout this dissertation as limited specifically *at the Amazon River* to one of the two regions constitute a subset of the species indicated in the Region column, and they are indicated in the Amazon column.

2. There are a number of species identified in the Region column as being limited either north or south of the Amazon River, but that did not show a statistically significant (regional) effect in the River column. These were typically species that, while only known to be distributed in one region, and only detected at sites in that region, were only detected at a few sites. Indicator Species Analysis will not result in a significant association with a particular group of sites if the species is not consistently observed at most sites in the group; this is a desirable property for a good test of group association.

3. *Crypturellus obsoletus*. This species identification is highly tentative. Audio recordings were made at the Siete de Julio site of unknown vocalizations of two counter-calling individuals, and were later tentatively identified under expert review as "a tinamou closely related to *C. obsoletus*" (BM Whitney, pers. comm.). The recordings compare favorably with examples of *C. obsoletus* vocalizations, yet that species is not known to occur within several hundred kilometers of the study sites. The vocalizations cannot be otherwise attributed to any other species in the dataset, so the taxon was retained as a distinctive species for analyses despite its uncertain identity. The recordings may eventually be found to represent an extension of the (already highly disjunct) range of *C. obsoletus*.

4. *Leucopternis melanops*. This species' distribution was until recently thought to be limited at the Amazon River, and current range maps reflect this, but the range apparently extends well to the south of the river, at least in Brazil (Amaral et al. 2007). One southern specimen from Brazil is from a site very near the Peruvian border. Its status in Amazonian Peru seems to be poorly enough known that it should not be assumed to be limited to sites north of the Amazon.

5. *Leucopternis semiplumbeus*. A single detection of this taxon was made at the Nuevo Valentin site. Its identification as *L. semiplumbeus* is tentative, because the taxon present in Amazonian Peru may represent an undescribed *Leucopternis* species closely related to *L. semiplumbeus*. In either case, it is certainly distinctive from other species in the dataset.

6. *Pyrrhura picta*. This species occurred at all sites south of the Amazon River, most of which are near, but outside, the poorly known distribution in Peru. *P. roseifrons* is considered the widespread *Pyrrhura* parakeet south of the Amazon in this region, but it was not observed at any site. *P. picta* is here considered to be limited at the Amazon because it does not occur north of the river, and its occurrence at sites to the south and west of its known distribution, along the south bank of the river, corroborate the northern limit at the river further to the east, which is depicted in Schulenberg et al. (2006).

7. *Phaethornis bourcieri*. This species is known to range south of the Amazon River in the study area, but I did not observe it at any of the southern survey sites, where *P. philippii* normally occurred. Nonetheless, *P. bourcieri* was considered to range on both sides of the Amazon, while *P. philippii* was considered to be limited at the Amazon, in accordance with Schulenberg et al. (2006).

8. *Heliodoxa schreibersii*. The known distribution of this species is north of the Amazon River, but I observed it at sites south of the river. Its distribution is currently represented as having a limit specifically at the Amazon for only a short distance east of the Napo River, whereas its limit through most of the study area is well to the north of the river. Given those limits (Schulenberg et al. 2006), and given that it appears to actually cross the river, I did not consider it to have a limit specifically at the river.

9. *Trogon melanurus*. As discussed elsewhere in this dissertation, *T. melanurus* appears to consist of two widespread, locally parapatric taxa in Loreto, probably separable at the species level. Each occurs on sites on both sides of the Amazon, in appropriate habitat. Trogon *melanurus* refers to the slow-vocalization form found in terra firme forest on nutrient-rich soils and in flooded forest, and *T.* [*melanurus*] refers to the fast-vocalization form found in terra firme forest on nutrient-poor soils.

10. *Herpsilochmus species novum*. As discussed elsewhere in this dissertation, a previously unknown Herpsilochmus antwren first collected at the Nuevo Esperanza site will be described as a distinct species. It is so far known only from sites near Nuevo Esperanza along the Apayacu, Ampiyacu, and Yaguasyacu Rivers, all to the north of the Amazon River. So little is currently known of its distribution that no judgment was made regarding its relation to the Amazon River.

11. *Heterocercus aurantiivertex*. This species occurs to the north of the Amazon River in Loreto, and is considered to be limited at the river throughout the study area. However, it is known to occur south and east of the Ucayali River, immediately west of the study region.

12. *Microcerculus marginatus*. This wide-ranging species does not consist of currently recognized subspecies with a boundary at the Amazon River, but it is considered to have a disjunction at the river that has not as yet been sufficiently described in the literature (e.g., Ridgely and Tudor 1989, T. Schulenberg pers. comm.). Consistent differences in the song on opposite banks of the Amazon are described in Schulenberg et al. (2007), and were observed and recorded at the study sites. I treat the taxon here as a single species, in keeping with the current SACC (2007) status. However, because there is a widely recognized and important disjunction, I treat the species as comprising two subspecies in the study area, with the boundary between them at the Amazon River. The subspecific names *marginatus* and *bolivianus*, corresponding to the northern and southern types, were synonymized by Peters (Mayr and Greenway 1960), and are not necessarily the names that would apply, were the two taxa formally separated.

Appendix 2. Twenty-nine bird species were excluded from analyses. There were some species included in analyses that probably have seasonal migrations despite the presence of some individuals at all times of year, but whose migration patterns are not well known.

Family, *Species*	Reason for exclusion from analyses
Ciconiidae	
Mycteria americana	Fly-over only
Cathartidae	
Cathartes melambrotus	Fly-over only
Coragyps atratus	Fly-over only
Accipitridae	
Elanoides forficatus	Fly-over only
Ictinia plumbea	Fly-over only
Leucopternis albicollis	Fly-over only
Buteo platypterus	Fly-over only; Seasonal migrant
Buteo swainsoni	Fly-over only; Seasonal migrant
Falconidae	
Milvago chimachima	Fly-over only
Columbidae	
Claravis pretiosa	Detected only after day 8 at one site
Psittacidae	
Ara macao	Fly-over only
Brotogeris versicolorus	Fly-over only
Cuculidae	
Coccyzus americanus	Seasonal migrant
Apodidae	
Chaetura cineriventris	Fly-over only
Chaetura egregia	Fly-over only
Chaetura brachyura	Fly-over only
Tachornis squamata	Fly-over only
Panyptila cayennensis	Fly-over only
Tyrannidae	
Contopus virens	Seasonal migrant
Myiodynastes luteiventris	Seasonal migrant
Myiodynastes maculatus	Seasonal migrant
Empidonomus aurantioatrocristatus	Seasonal migrant
Cotingidae	
Xipholena punicea	Detected only after day 8 at one site
Vireonidae	
Vireo olivaceous	Seasonal migrant
Vireo flavoviridis	Seasonal migrant
Hirundinidae	
Progne elegans	Fly-over only; Seasonal migrant
Turdidae	
Catharus ustulatus	Seasonal migrant
Thraupidae	
Piranga olivacea	Seasonal migrant
Fringillidae	
Euphonia chlorotica	Detected only after day 8 at one site

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VITA

Lazarus Yates Pomara was born in Dallas in 1972. Lars was raised along with his older brother in rural northern Arkansas, among other places, and then attended the University of Dallas in Irving, TX. After some serious dabbling in art and music, he received a BS in biology. He then spent three years independently studying birds, with a double minor in plants and guitar, while employed by a number of field ecology research projects throughout the United States. His real interest was in the tropics, though, and after a few visits to Thailand, he landed a job studying birds in the Republic of Panama with the Smithsonian Migratory Bird Center. This work eventually transformed into a master's thesis at the University of Georgia in Athens, where Lars studied wildlife ecology at the Warnell School of Forestry and Natural Resources. His MS thesis dealt with the mixed-species flocking behavior of birds in shade coffee fields and montane forest. Lars then worked in the GIS lab at PRBO Conservation Science in Point Reyes National Seashore, CA for nearly two years, developing geographical analysis skills, making maps, and contributing to several avian conservation research projects. He entered the PhD program of the Department of Geography at the University of Texas at Austin in 2003, and hopes to continue researching South American biogeographic diversity for the foreseeable future.

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